1986

Variations In The Biennial Life History Strategy Among 15 Ruderal Species In An Abandoned Gravel Pit Near London, Ontario

Paul Frederick Threadgill

CANADIAN THESES

THÈSES CANADIENNES

NOTICE

The quality of this microfiche is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us an inferior photocopy.

Previously copyrighted materials (journal articles, published tests, etc.) are not filmed.

Reproduction in full or in part of this film is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30.

AVIS

La qualité de cette microfiche dépend grandement de la qu de la thèse soumise au microfilmage. Nous avons tout fait assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'un sité qui a conféré le grade.

La qualité d'impression de certaines pages peut laiss désirer, surtout si les pages originales ont été dactylograph à l'aide d'un ruban usé ou si l'université nous a fait par une photocopie de qualité inférieure

Les documents qui font déjà l'objet d'un droit d'auteur (art de revue, examens publiés, etc.) ne sont pas microfilm

La reproduction, même partielle, de ce microfilm est sou à la Loi canadienne sur le droit d'auteur, SRC 1970, c C

THIS DISSERTATION HAS BEEN MICROFILMED EXACTLY AS RECEIVED

LA THÈSE A ÉTÉ MICROFILMÉE TELLE QUE NOUS L'AVONS REÇUE

VARIATIONS IN THE BIENNIAL LIFE HISTORY STRATEGY AMONG 15 RUDERAL SPECIES IN AN ABANDONED GRAVEL PIT NEAR LONDON, ONTARIO

by

Paul Frederick Threadgill

Department of Plant Sciences

Submitted in partial fulfillment

of the requirements for the degree of

Doctor of Philosophy

Faculty of Graduate Studies

The University of Western Ontario

London, Ontario

August, 1986

ISBN 0-315-33001-5

ABSTRACT

Fifteen biennial species co-existed in an abandoned gravel pit near London, Ontario. Investigations were performed to identify variations in their regeneration characteristics. Once identified, variations were compared to attempt to explain these species' co-existence in this habitat. Mean net seed production per plant, mean seed weight per species, and dispersal of diaspores by wind, water, and animals were determined for each species. Mean seed production per plant ranged from 119 to 22,425. Mean weight per seed per species ranged from 0.07mg to 13.03mg. Mean weight per seed varied throughout the growing season in each of thirteen species. Diaspores of eight species had no morphological adaptation for dispersal, five were adapted for wind dispersal, and two for external carriage by animals. Diaspores of all species floated; those of thirteen floated after agitation. Greater numbers of diaspores of two species adhered to a dry groundhog pelt whereas greater numbers of those of thirteen species adhered to a wet pelt. The biennial seed rain within the study area was assessed using a grid of sticky traps. The biennial seed bank was assessed through collection and subsequent incubation of soil cores. Viable ungerminated seeds present in two collections were extracted. Both seed rain and seed bank were dominated by two taxa. Six species formed persistent, and two transient, seed banks. Seeds of six species were nondormant; a portion of those of four were nondormant, and those of five were innately dormant. Seeds of each species were sown in both sparsely and densely vegetated plots. Seedling emergence was greater in dense plots for four species but in sparse plots for the others. Mean percentage seedling establishment ranged from 0 to 83% in sparse plots and from 0 to 92% in dense plots. Seeds of all species were sown into a range of gap sizes and soil textures. More seedlings of five taxa established on medium to fine textures whereas more seedlings of six species established on medium to coarse textures. More seedlings of all species established in the three largest gaps. These species differed in every life history characteristic investigated.

This thesis is dedicated to my parents, Mr. and Mrs. C.W. Threadgill, and to my maternal grandmother, Mrs. Mary E. Fleenor.

ACKNOWLEDGEMENTS

Any project which involves a great deal of planning, research, observation and experimentation both in the field and in the laboratory, reduction and analysis of data, drafting, photography, writing, typing, editing, and duplication is beyond the capability of a single individual to successfully complete. Consequently, I am deeply indebted to a large number of people through whose combined efforts this dissertation became possible. At this time I would like to gratefully acknowledge their contributions and extend to them my heartfelt appreciation for their respective roles in this project.

To Dr. P.B. Cavers for advice, consultation, encouragement, criticism and especially support throughout all stages of the project.

To Dr. R.C. Jancey and Dr. M.A. Maun for advice and criticism particularly at the initial and final stages of the project.

To Mr. Dan Worton of Standard Aggregates Inc. for permission to carry out my study in one of their abandoned pits.

To the members of the West Nissouri Township Council for allowing me access to their active pit.

To Dr. J.E.H. Martin of the Agriculture Canada Biosystematics Research Institute for the identification of the lepidopteran stem borers which infested *Onopordum acanthium*.

To Dr. K.L. Gross, Dr. K.M. Klemow, Dr. J.S. Millar, Dr. D.M. Scott, Mr. G.J. Umphrey, Mr. K.G. Gerow, Dr. R.J. Robertson, Dr. P.J. Weatherhead, Dr. S.E. Weaver and Mr. W.G. Stewart for sharing their expertise on particular issues which arose during this study.

To Doris Rowley, Muriel Andrae, Marion Steel, Rob Gushe, Jim O'Toole, Graham Sudbury, Silvester Vicic, Judith Quigley, Helen Kibblewhite, Miriam Bee, Roger Chum, Sarah Rang, Sarah Davis, Anne Scotchbrook, Ron Anderson, John Budge, Scott Murphy, Cathy Major and Peter Duenk

for their aid in one to several aspects of the field research or data analysis.

To Jane Arnott for mounting voucher specimens.

To Amy McGrath for drafting figures.

To Marguerite Bough for drafting figures, criticism, and particularly for creating the sketches of seedlings which appear in Chapter 5.

To Irene Krajnyk for drafting figures and for always being able to provide me with the facilities or equipment I needed to solve a particular problem.

To Alan Noon for the photoreduction of figures and production of slides.

To Dr. A.F. Stairs and Brenda Frick for criticism of the final draft of the thesis.

To Dr. P.G. Smith for untiring assistance with recalcitrant word-processing software and for criticism of the final draft of the thesis.

To Dr. R.E. Hinson for encouragement and support throughout the bulk of the project as well as criticism of the final draft of the thesis.

Finally, particular thanks are due to Debbie Burkholder without whose advice, support and untiring assistance in data analysis, typing, editing and duplication, this thesis would have never been completed.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

Chapter 1

Introduction

Smith's (1927) investigation of the occurrence of an annual race and the inheritance of annuality in the otherwise biennial *Melilotus alba* was one of the earliest studies which focussed on the life history strategy of a biennial species. Afterwards this field lay dormant for nearly 50 years until Holt (1972), in his study of the seedling dynamics of early successional plants, concentrated on *Daucus carota*, a biennial species. Approximately simultaneously with Holt's study, a series of life history studies began to appear which dealt with long-lived monocarpic perennial plant species (*e.g.*: Beattie et al. 1973, Schaffer and Gadgil 1975, Janzen 1976, Inouye and Taylor 1980, Threadgill et al. 1981, Young 1984), but with the exception of Dale's (1974) review of the life history characteristics of *Daucus carota*, no further research was performed with a biennial species until the seminal population studies of *Dipsacus sylvestris* by Werner (1975a,b,c,d; 1977). In 1977, Harper (1977) noted that so few population biology studies had been conducted which involved biennials that it was impossible to make generalizations concerning species which employ this life history strategy. At the same time Hart (1977) reported that biennial species were rare in the North American flora and used life history optimization models in the manner of Gadgil and Bossert (1970), Charnov and Schaffer (1973), and Schaffer and Gadgil (1975) to offer an explanation for their rarity. Immediately following the publication of Hart's paper, many others followed which presented, modified, and refined mathematical models to describe the biennial life history strategy and to

explain the occurrence of biennials (*e.g.*: Werner and Caswell 1977, Caswell and Werner 1978, Hastings and Caswell 1979, Silvertown 1982, Caswell 1982, Lacey et al. 1983, Hirose 1983, Silvertown 1983, Klinkhammer and de Jong 1983, Thompson 1984, and Kelly 1985b). These mathematical treatments dealt with all biennial species as a monolithic group and so gave the impression that all biennial species, because of their common, tightly-defined life history strategy, employed virtually identical tactics (*sensu* Harper 1977).

In the meantime, a great deal of research was being performed on the population biology of biennial species. Several researchers investigated the population biology of individual species (*e.g.*: Prince et al. 1978, Gross and Werner 1978, Turkington et al. 1978, van der Meijden and van der Waals-Kooi 1979, Baskin and Baskin 1979 a,b, Cavers et al. 1979, Gross 1980b, Gross et al. 1980, Lacey 1981, van Leeuwen 1981, Klemow and Raynal 1981, Marks and Prince 1981, Marks and Prince 1982, Prince and Marks 1982, Lacey 1982, Gross and Werner 1983, Lacey and Pace 1983, Reinartz 1984 a,b). Others took a comparative view of several biennial species when they occurred within the same habitat. Gross (1981) and Gross and Werner (1982) examined 4 species which appeared sequentially in time in old fields in southern Michigan. They investigated the passage of juveniles into maturity (Gross 1981) and compared percent seedling emergence, percent seedling establishment, seed weight and seedling morphology with the ability to colonize gaps of various sizes (Gross and Werner 1982). Several studies have been carried out on biennial species which inhabit dune systems in the Netherlands. Van Leeuwen and van Breeman (1980) looked at seed production per plant, seed dispersal, and seed longevity in the soil for four species. Van Breeman and van Leeuwen

(1983) compared the longevity of seeds of 3 species in the seed bank. In addition, van Breeman (1984) investigated 3 species for seed predation, seed bank dynamics, seedling emergence, and seedling establishment in the field and tested the seed germination requirements of the same 3 species in the laboratory. In the same dune system de Jong and Klinkhammer (1986) compared seed production per plant, seed predation, seed dispersal, seedling emergence, seedling survivorship, seedling establishment, and the passage of juveniles into maturity for 2 species. Verkaar and Schenkeveld (1984a) examined seed production per plant, percent seedling emergence, number of seedlings produced per parent, and survival of seedlings in 4 species in chalk grasslands in the Netherlands. Then, using the same species in the same habitat, they compared seed output in relation to nutrient availability (Verkaar and Schenkeveld 1984b). Klemow and Raynal (1985) investigated seed production per plant, seedling emergence, seedling survivorship, seedling establishment, and the passage of juveniles into maturity in 2 species in an abandoned limestone quarry in New York. Finally, Gross (1984), in a greenhouse study, examined the effect of seed size and seedling morphology on seedling emergence and seedling establishment in 6 species. Since Harper's statement (1977), sufficient research has been carried out on the population biology of various biennial species that a picture has emerged of the breadth of tactics which biennial species employ in the execution of their common life history strategy.

The nature of the biennial life cycle strategy restricts the types of habitats that species that employ it can exploit. Because they are semelparous and relatively short-lived, biennials are soon displaced from

undisturbed habitats by perennial species which form a closed canopy and thereby prevent germination of their seeds or establishment of their seedlings (Hart 1977, Harper 1977). Biennial species are also excluded from annually disturbed habitats because they are prevented from completing their two-stage life cycle (Hart 1977, Harper 1977). As a group, biennial species occur consistently in a few types of habitat. They are found in productive, intermittently-disturbed vegetation such as woodland gaps, old fields, or mud and shingle shores; in semi-open habitats such as chalk grasslands, short turf, or grazed lands; and in unproductive open areas such as abandoned gravel pits, abandoned limestone quarries, cedar glades, dune systems, and moraines (Salisbury 1961, Viereck 1966, Young and Evans 1969, Holt 1972, Dale 1974, Werner 1975a,b,c, Grubb 1976, Harper 1977, Hart 1977, Werner 1977; Gross and Werner 1978, Turkington et al. 1978, Hawthorn and Hayne 1978, Grime 1979, Baskin and Baskin 1979a,b, van der Meijden and van der Waals-Kooi 1979, Cavers et al. 1979, Gross et al. 1980, van Leeuwen and van Breeman 1980, Gross 1980b, Gross 1981, Heagy 1981, Klemow and Raynal 1981, Lacey 1981, van Leeuwen 1981, Gross and Werner 1982, Lacey 1982, Lacey and Pace 1983, van Breeman and van Leeuwen 1983, van Breeman 1984, Reinartz 1984a, Klemow and Raynal 1985, Kelly 1985b, de Jong and Klinkhammer 1986).

Given that biennial species as a group have a very narrow set of environmental conditions within which they can establish and maintain their populations, it might be assumed that they are functionally very nearly identical and that their ecological requirements must be very similar. In nature, however, habitats which are suitable for biennials are often occupied by from two to several species (Grubb 1976, van Leeuwen and van Breeman

1980, Gross 1981, Klemow 1982, Gross and Werner 1982, van Breeman and van Leeuwen 1983, van Breeman 1984, Klemow and Raynal 1985, de Jong and Klinkhammer 1986). The question then arises, how can several species, which are apparently ecologically very similar, partition their common habitat so they are able to co-exist?

The distribution and abundance of mature plants within a given community at a given time are the result of events which took place when seeds and seedlings of the component species were present (Grubb 1977, Harper 1977, Werner 1977, Cook 1979, Werner 1979, Gross and Werner 1982, Gross 1984, de Jong and Klinkhammer 1986). Many studies have shown that these stages of the life cycle of a plant are extremely vulnerable to adverse environmental conditions, to predation, and to competition, both with other emerging seedlings and with established vegetation (Darwin 1860, Harper 1967, Naylor 1972, Sarukhan and Harper 1973, Sharitz and McCormick 1973, Harper and White 1974, Dale 1974, Kawano and Nagai 1975, Werner 1975a,b, Hawthorn and Hayne 1978, Mack 1976, Symonides 1977, King 1977b, Werner 1977, Werner and Caswell 1977, Turkington et al. 1978, Cavers et al. 1979, Baskin and Baskin 1979a,b, van der Meijden and van der Waals-Kooi 1979, Cook 1979, Hickman 1979, Werner 1979, Gross 1980a,b, Schaal 1980, Klemow and Raynal 1981, Silvertown and Dickie 1981, Marks and Prince 1981, Gross and Werner 1982, Cavers 1983, Verkaar and Schenkeveld 1984a, Young 1984, Klemow and Raynal 1985, de Jong and Klinkhammer 1986). Consequently, it is the interactions of seeds and seedlings with the physical and biotic environments that determine which individuals among the large numbers of seeds which are dispersed within a community will germinate, emerge, and

establish successfully to take a place in that community.

Grubb (1977) has termed the process through which new individuals of a species enter a community "regeneration". The stages of the plant life cycle which Grubb (1977) believes to be most critical to successful regeneration are: production of viable seeds, dispersal of diaspores, seed germination, seedling emergence and establishment, and passage of the juvenile into maturity. These life cycle stages he refers to collectively as the elements of a plant's "regeneration niche" (Grubb 1977).

Previous studies have shown that biennial species are suprisingly variable in their life history characteristics, including those which compose Grubb's regeneration niche. A few examples should demonstrate this variability. Diaspores of biennial species range from those such as *Dipsacus sylvestris* which have no morphological adaptation for dispersal (Werner 1975a) to those such as *Arctium minus* which have hooks and barbs for adhering to animal fur (Gross et al. 1980), to those such as *Cirsium vulgare* which have relatively large intricate pappi to bear them on wind currents (de Jong and Klinkhammer 1986). Mean seed production among biennial species has been shown to range from 120 seeds/plant for *Tragopogon dubius* (Gross 1980a), to 350,000 seeds/plant for *Melilotus alba* (Turkington et al. 1978). Mean seed size has been found to vary among biennial species from 0.05mg in *Verbascum thapsus* (Gross 1984) to 12.4mg in *Onopordum acanthium* (Cavers and Steel 1984). Some biennial species, such as *Alliaria petiolata*, have seeds which are deeply dormant at maturity (Cavers et al. 1979). A few seeds of some others such as *Daucus carota*, are capable of germination at maturity, but the larger portion are innately dormant (Dale and Harrison 1966),

whereas some, such as *Dipsacus sylvestris*, produce seeds which are not dormant at maturity, but which can rapidly be induced into secondary dormancy by environmental conditions (Werner 1975a). Some biennial species, such as *Picris hieracioides*, do not form persistent seed banks (Klemow and Raynal 1985). Others, such as *Tragopogon dubius*, form transient seed banks (*sensu* Thompson and Grime 1979) which are only present during one season of the year. Other biennial species such as *Daucus carota*, form relatively small persistent seed banks (*sensu* Thompson and Grime 1979), and yet other species such as *Verbascum thapsus*, form relatively large persistent seed banks (Reinartz 1984b). The seeds of *Tragopogon dubius* live for less than a year in the soil (Gross 1984), whereas those of other biennial species such as *Verbascum blattaria* and *Verbascum thapsus* may remain viable for up to 100 years in the soil (Kivilaan and Bandurski 1981). The seedling morphology of biennial species ranges from the long grass-like leaves of *Tragopogon dubius* to the small flat rosettes of *Verbascum thapsus* (Gross 1984). Finally, as many as 86% of emerged seedlings of *Daucus carota* have been reported to establish in an *Andropogon* sod in southern Michigan (Holt 1972) whereas in some years, none of the seedlings of *Cirsium vulgare* which emerged in a dune system in the Netherlands successfully established (de Jong and Klinkhammer 1986).

Given the great variation in life history characteristics present among biennial species in general, I was curious as to whether or not the co-existence of several biennial species in a given habitat could in fact be the result of differences in their regeneration characteristics. Heagy (1981) reported that 15 biennial species occurred concurrently in a stable, open

ruderal community in an abandoned gravel pit near London, Ontario. A preliminary investigation revealed that all of these species appeared to be very similar in life-form, adult phenology, and habitat range. This abandoned gravel pit provided an excellent system in which to pursue two related lines of inquiry: 1) what is the range of variability in tactics (*sensu* Harper 1977) employed among species which have a biennial life history strategy and, 2) are very similar species able to co-exist through differentiation in their regeneration characteristics?

Several investigations of each of the 15 biennial species were carried out to determine the number of viable seeds produced, dispersal of diaspores, dormancy and germination behavior of seeds, and emergence and establishment of seedlings. The last of the elements of Grubb's (1977) regeneration niche, passage of the juvenile into maturity, was not included in these investigations because several studies involving biennial species had shown that once a seedling had established successfully, the risk of mortality was substantially reduced until flowering (Werner 1975c, van der Meijden and van der Waals-Kooi 1979, Gross 1981, Klemow and Raynal 1981, Klemow and Raynal 1985, Klinkhammer and de Jong 1986). Once these regeneration characteristics had been quantified for each biennial species, they were compared in an attempt to identify interspecific variations. If variations in any regeneration characteristics were found between species, these were examined to determine whether or not the variation present could partially account for the continued co-existence of the biennial species in the gravel pit.

For the purpose of these investigations, a biennial was defined as a plant species which is semelparous and which has the potential to complete its life cycle within two years but which is incapable of doing so within one. Implicit in this arbitrary definition is the full understanding that some of the species included have genetically annual races (Smith 1927, Lacey et al 1983), that some have the capability to behave as winter annuals (Harper 1977, Prince et al. 1978), and that some vary from annual to biennial to triennial with increasing latitude or elevation (Smith 1927, Reinartz 1984a). I considered this to be inherent natural variation. Virtually every individual of each species included in the study however, behaved in the study area as a biennial according to the above definition.

There are three points of contrast between previous studies and mine. First, previous investigations have compared relatively few species. The study which included the most species, 6, was performed in a greenhouse (Gross 1984). The field studies compared at most 4 species (Gross 1981, Gross and Werner 1982, van Leeuwen and van Breeman 1980, Verkaar and Schenkeveld 1984a, Verkaar and Schenkeveld 1984b). A second difference is in the habitats where the studies were carried out. The only other study performed in an open, unproductive habitat was that of Klemow and Raynal (1985) whose work involved 2 species and did not include an investigation of seed bank dynamics. Finally, when seeds were introduced in every other study, they were introduced into plots of single species and the results from these plots were compared. In my study, when seeds were introduced into plots in the field to assess seedling emergence, survivorship, and establishment; seeds of all 15 species were introduced into each plot. This

procedure simulated the seed rain and allowed me to observe how the seeds and seedlings of the 15 biennial species behave *vis-a-vis* one another as they do in the field. My work, then, complements existing studies in that a larger number of species were compared, many times in novel treatments, in a habitat different from those where previous studies were carried out. It thereby serves to broaden existing knowledge both of the means by which biennial species are able to co-exist in stable, open, unproductive habitats and of the variations in regeneration characteristics which are present among biennial species.

This thesis is presented as seven separate but interrelated chapters. The second describes the species which were studied and the study area. The third examines the production of viable seeds, variation in seed weight and dispersal of diaspores of each of the 15 biennial species. The fourth describes the germination behavior of each species in a controlled environment, and the seed rain and seed bank dynamics of the 15 species taken as a group in the field. The fifth examines the emergence, survivorship, and establishment of seedlings of the 15 species sown as a group in plots in the field. The sixth describes two experiments designed to investigate the emergence, survivorship, and establishment of the 15 species sown as a group onto plots of various surface texture and into gaps of various sizes which had been created in a background vegetation. Each chapter has been written as a separate manuscript. Consequently some material that is presented in earlier chapters is repeated in later chapters. The thesis is concluded by an overall synthesis.

Chapter 2

Description of the biennial species and the study area

2.1 The biennial species

The 15 biennial species included in these investigations are presented in Table 2.1. They are a taxonomically diverse group, representing eight families and seven orders. All are introduced species (Gleason and Cronquist 1963) with the exception of *Oenothera biennis* which is native to southwestern North America (Cleland 1972). All are relatively tall, coarse herbs with flowering periods which extend over several weeks. Phenological observations were made in the study area for each of the 15 biennial species during the 1980, 1981, and 1982 growing seasons. The location of emerging seedlings for most species proved difficult at best. Generally, emerged seedlings of a given species were identified some time after their emergence, and so the approximate date of emergence was not estimated. Juveniles and bolting individuals of all species were readily identifiable and appeared early in the spring soon after the ground thawed. There was wide variation among the biennial species in both the timing of the start of flowering and the timing of seed maturation. *Tragopogon dubius*, *Tragopogon pratensis*, and *Alliaria petiolata* began to flower from mid to late May. Seeds of both *Tragopogon* species were mature in mid- to late June, whereas those of *Alliaria petiolata* were mature by mid-July. *Melilotus officinalis*, *Echium vulgare*, and *Melilotus alba* each began to flower from late May to early June but the timing of seed maturation varied among them. Mature seeds

Species	Family	Order
Alliaria petiolata (Bieb.)Cavara and Grande	Cruciferae	Papaverales
Melilotus alba Desr.	Fabaceae	Rosales
Melilotus officinalis (L.) Lam.	Fabaceae	Rosales
Oenothera biennis L.	Onagraceae	Myrtales
Daucus carota L.	Umbelliferae	Umbellales
Echium vulgare L.	Boraginaceae	Polemoniales
Verbascum blattaria L.	Scrophulariaceae	Polemoniales
Verbascum thapsus L.	Scrophulariaceae	Polemoniales
Dipsacus sylvestris Huds.	Dipsacaceae	Rubiales
Arctium minus (Hill) Bernh.	Compositae	Asterales
Cirsium vulgare (Savi)Ten.	Compositae	Asterales
Lactuca scariola L.	Compositae	Asterales
Onopordum acanthium L.	Compositae	Asterales
Tragopogon dubius Scop.	Compositae	Asterales
Tragopogon pratensis L.	Compositae	Asterales

Table 2.1. Scientific names and taxonomic affiliations of 15 biennial species which are present within the Marshall pit. Nomenclature follows Alex et al. (1980). Voucher specimens of each of these species have been deposited in the University of Western Ontario herbarium (UWO).

of *Echium vulgare* were present in early July, those of *Melilotus officinalis* in late July and those of *Melilotus alba* in early August. *Onopordum acanthium*, *Daucus carota*, *Arctium minus*, *Verbascum blattaria*, and *Verbascum thapsus* began flowering from late June to early July and again the timing of seed maturation varied widely among these species. Mature seeds of *Onopordum acanthium* were present by late July, those of both *Daucus carota* and *Verbascum thapsus* were present in early August, those of *Arctium minus* in mid-August and those of *Verbascum blattaria* in mid-September. *Oenothera biennis*, *Dipsacus sylvestris*, and *Cirsium vulgare* began to flower in mid-July. Mature seeds of *Cirsium vulgare* were present by late July whereas those of both *Oenothera biennis* and *Dipsacus sylvestris* were not present until mid-September. *Lactuca scariola* began to flower in early August and had produced mature seeds by late August. Diaspores of each of these species began to disperse immediately after ripe seeds had appeared, and some individuals of each species were observed to continue dispersing diaspores within the study area through November, at which time observations ceased for the winter.

2.2 The study area

A. The sampling grid

The field study site where these investigations were performed was an extensive, variable slope approximately 0.26 ha in area formed by the embankment of a relict access road. It had north and northeastern exposures, and was located in the northeastern corner of an abandoned open pit gravel mine (henceforth referred to as the Marshall pit). A grid system

was created throughout the study area to facilitate the siting of exact points within the study area and to provide a uniform framework for systematic sampling. This grid was established by means of 30' transit and a 50m chain. All distances within the grid were level-chained.

In the establishment of the grid, a permanent transect was established parallel to the contour of the embankment slope. This transect extended from the fence corner of an adjacent lot, which was arbitrarily selected as the northern boundary of the study area, for 60m to the termination point of the relict access road, which had been selected arbitrarily as the southern end of the study area. This transect formed the western edge of the study area. This and all subsequently established permanent transects were marked by driving a 26cm eavestroughing nail flagged with plastic ribbon into the ground beginning at the 0 point and continuing at each 5m interval through the length of the transect. A second permanent transect was established perpendicular to the first which originated at the 0 point of transect one and extended 40m to the toe of the embankment slope. This had been arbitrarily selected as the eastern end of the study site. This latter transect marked the northern edge of the study area. Eight additional permanent transects were established, one at each 5m interval along the second permanent transect. Each of these was perpendicular to the second transect and parallel to the first. The eighth of these transects lay at the toe of the embankment slope and formed the eastern edge of the study area. The fourth through the ninth horizontal transects extended southwards for 70m because of the configuration of the embankment slope. Finally, a series of 15 permanent transects was established perpendicular

to the contour of the embankment slope, each extending along the 5m interval points of the previously established horizontal transects. This system of transects taken in total provided a sampling grid of one hundred and six 5m x 5m squares which were used repeatedly throughout the study period as a framework for sampling in the vegetation surveys, seed rain survey, and seed bank survey.

B. Location

The Marshall pit was approximately 21 ha in area and at the time of these investigations was approximately 7 years of age since abandonment (Hewitt and Cowan 1969, Heagy 1981). It was located on Fanshawe Park Road, lots 3 and 4, London township, Middlesex County, Ontario (Hewitt and Cowan 1969); this is approximately 43°03'08" N and 81°11'11" W.

C. Physiography

London Township lies in what Chapman and Putnam (1966) categorize as the Caradoc Sand Plains physiographic region. The bedrock which underlies London Township is of Devonian origin and belongs to the Delaware formation (Chapman and Putman 1966). The surface features, however, including the gravel deposits which were mined to produce the Marshall pit, are the product of the Wisconsin glaciation (Chapman and Putnam 1966). These gravel deposits are outwash from the great Thames spillway which carried drainage during the time that the glacier stood at the Ingersoll moraine (Chapman and Putnam 1966)

D. Substrate characteristics

At the time of my study, soil development in the Marshall pit had not produced discernible horizons. The substrate in the study area was therefore a regosol (Webber and Hoffman 1967). In June of 1981 a series of cores was collected from the substrate systematically throughout the study area (see 4.2 C.). The term "soil core" is not applicable in this case since there was no horizon development. Once collected, all cores were delivered to the Ontario Ministry of Agriculture and Food Soil Testing Laboratory at the University of Guelph where each was assessed for texture, pH, and total phosphorus, potassium, and magnesium. The fraction of each core which passed through a 2 mm sieve was the portion analyzed.

The fine fraction of each core from the study area was coarse textured and basic, having a mean pH of 7.8 ± 0.2. Heagy (1981) also found that the substrate of the south-facing slope of the Marshall pit was coarse textured and basic. She reported that in 90% of her substrate cores, less than 50% of the material would pass through a 2 mm sieve and that the mean pH of these samples was 7.5 ± 0.1 (Heagy 1981). Even though the mean pH of cores taken within my study area was slightly more basic than those reported by Heagy (1981) for the Marshall pit, it falls within the range of values she reported for the substrate within 4 other local gravel pits. The fine fraction of the substrate within my study area was relatively poor in the macronutrients which were analyzed. Phosphorus, potassium and magnesium were present at mean values of 12.8 ± 7.2 ppm, 68.7 ± 42.3 ppm, and 91.9 ± 24.3 ppm respectively. Heagy (1981) reported that these macronutrients were present in the substate of the south-facing slope of

the Marshall pit at mean levels of 21.0 ± 3.8 ppm for phosphorus, 107.0 ± 17.0 ppm for potassium, and 159.0 ± 16.0 ppm for magnesium. Thus, the mean values for each of these three macronutrients in the substrate of my study area were lower than those reported by Heagy (1981) for the Marshall pit, but were within the ranges she found in the substrates of 4 other local pits. In addition to phosphorus, potassium and magnesium, Heagy (1981) determined total calcium, total carbonates, percent organic matter, and the wilting coefficient for the substrates in the gravel pits in her study. She found that the substrate of the south-facing slope of the Marshall pit was rich in calcium (2740 ± 40 ppm) and total carbonates (1.1 ± 0.5% by weight), low in organic matter (3.8 ± 0.6% by weight) and had little capacity to retain water. Although these characters were not assessed in my study, it was probable that the substrate within the study area had similar values to those reported by Heagy (1981).

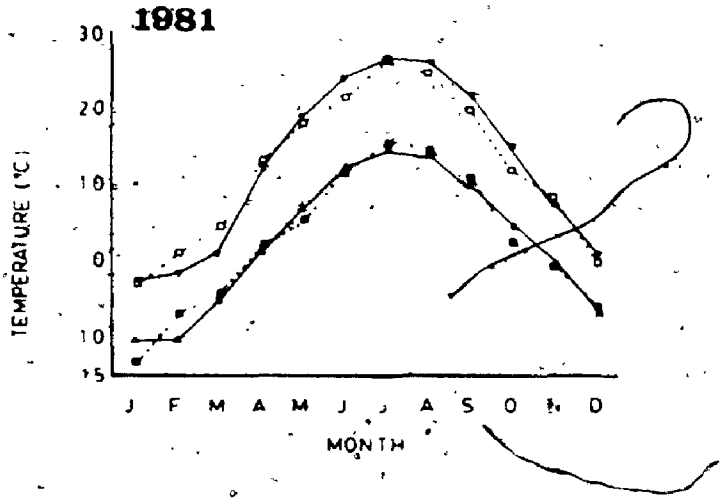
E. Climate

Middlesex County lies within Koppen's Dfa climatic zone (Ackerman 1941). This is an area of moist climate with severe winters and relatively long, hot summers.

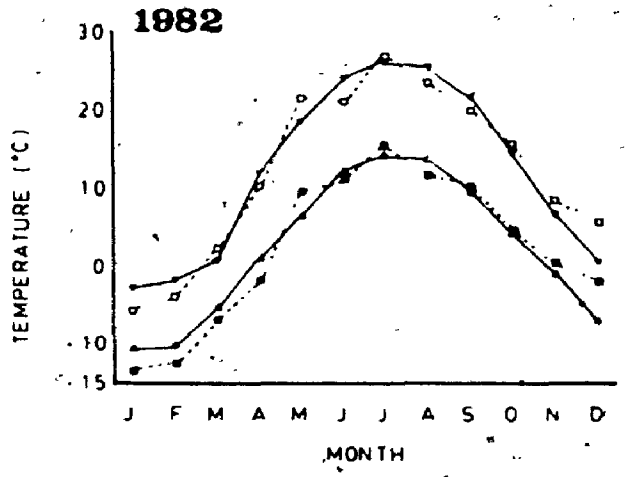
The local climate prevalent within the Marshall pit is reflected by the climatological data recorded by Environment Canada (1981a, 1981b, 1982, 1983) at the London Airport weather station. This station at approximately 3 km southeast is the closest official recording station to the study area. In Figure 2.1 the mean monthly maximum and mean monthly minimum temperatures for each year of the study are compared individually with the

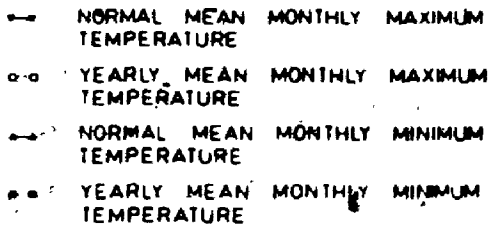
NORMAL AND MEAN MONTHLY MAXIMUM AND MINIMUM TEMPERATURES FOR LONDON, ONTARIO

A

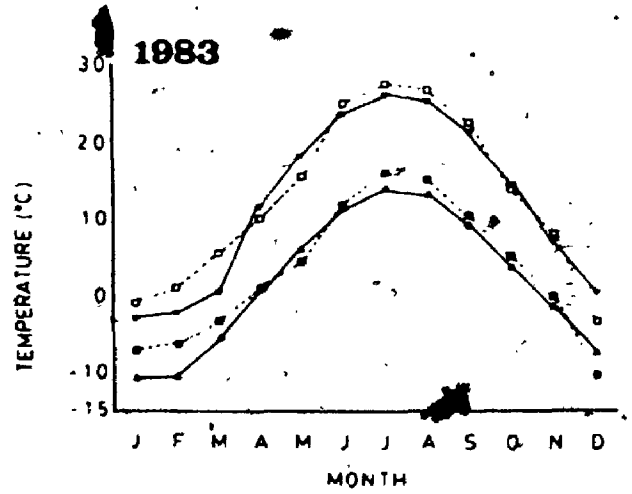


B





C



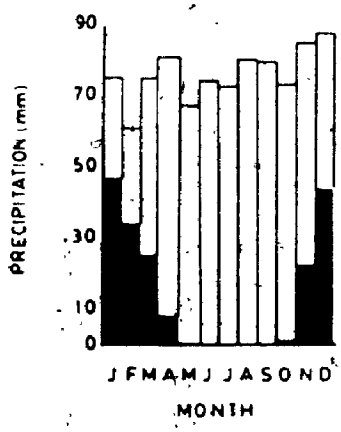
30 year (1951-1980) normal mean monthly maximum and mean monthly minimum temperatures. If only the months which make up the growing season, May, June, July, August and September, are considered, it can be seen that even though some yearly variation in temperature occurred, for example 1981 and 1982 were slightly cooler than normal whereas 1983 was slightly warmer than normal, there were no major deviations from the expected normal temperatures during the years of my study (Figure 2.1).

In Figure 2.2 the 30 year (1951-1980) normal mean monthly precipitation is presented along with the mean monthly precipitation for each of the years of my study. If one considers only the months which make up the growing season, the mean monthly precipitation was quite variable during this time (Figure 2.2). May was drier than expected in 1981, but the remainder of the growing season was wetter than normal with September being unusually wet (Figure 2.2). Precipitation in May, 1982 was normal, but June was unusually wet, July was unusually dry and the remainder of the growing season was wetter than normal (Figure 2.2). May of 1983 was very wet and the growing season was wetter than normal until September, which was drier than normal (Figure 2.2). Despite the monthly variation in precipitation within the three growing seasons, there were, with the possible exception of July 1982, no extended periods of drought which could have been expected to affect the emergence and establishment of seedlings in the field.

The prevailing wind in the London, Ontario area changes both in mean speed and direction throughout the year. It comes out of the west from October through February with mean speeds which range from 14.7 to 19.7 km/hr (Environment Canada 1981a). From March through May prevailing

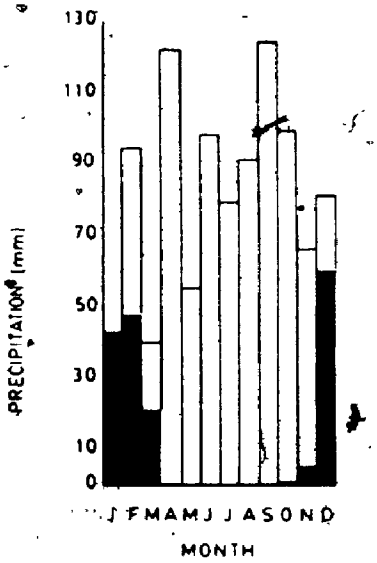
NORMAL MEAN MONTHLY PRECIPITATION FOR LONDON, ONTARIO

A



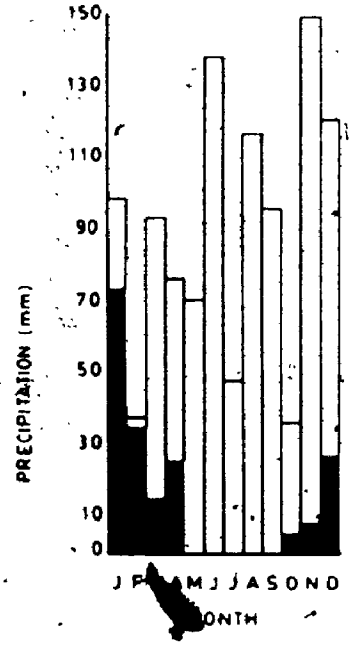
1981 MEAN MONTHLY PRECIPITATION FOR LONDON, ONTARIO

B



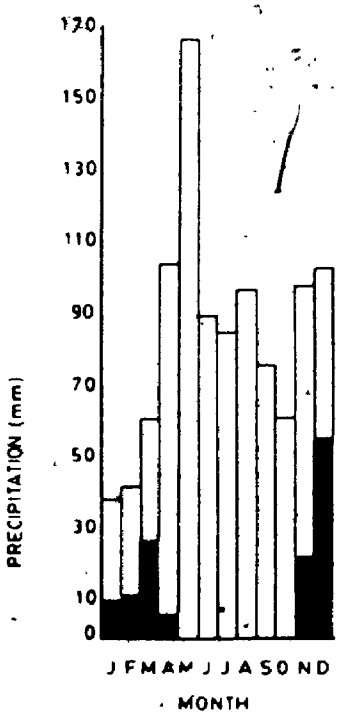
1982 MEAN MONTHLY PRECIPITATION FOR LONDON, ONTARIO

C



1983 MEAN MONTHLY PRECIPITATION FOR LONDON, ONTARIO

D



PERCENT TOTAL PRECIPITATION WHICH WAS SNOW

PERCENT TOTAL PRECIPITATION WHICH WAS RAIN

winds originate in the east and have mean speeds from 15.9 to 18.9 km/hr (Environment Canada 1981a). In June and July they come from the south at mean speeds of 11.8 to 13.5 km/hr (Environment Canada 1981a). The prevailing wind blows from the west in August at a mean speed of 11.5 km/hr (Environment Canada 1981a). In September it comes out of the east with a mean speed of 12.9 km/hr (Environment Canada 1981a).

No attempt was made during my investigations to collect microclimatic data for the study area. Some aspects of the microclimate, however, can be inferred from data recorded in other studies carried out in similar habitats. Heagy (1981) measured atmospheric evaporation rates throughout the growing season at the top, middle, and toe of the south-facing slope in the Marshall pit. While she found that the rates of evaporation near the top of the slope, in areas exposed to the wind, were relatively high, the evaporation rates for locations at the toe of the slope, a position similar to that of my study area, were surprisingly low.

Klemow (1982) found that on warm sunny days, the midday temperatures of exposed surfaces in an abandoned limestone quarry located approximately 400 km east of the Marshall pit exceeded 44 C and those of shaded surfaces could be as high as 35 C. Since the Marshall pit is at approximately the same latitude and altitude it is expected that similar surface temperatures could be reached within my study area.

F. Vegetation

London Township lies just within the northern boundary of what Rowe

(1972) defined as the Deciduous Forest Region of Canada. Within the Marshall pit, the process of natural revegetation which followed the devastation of mining has resulted in the development of a relatively open ruderal community composed largely of annuals, biennials, and herbaceous perennials. Important species present in this community, in addition to the 15 biennials listed in Table 2.1, are: *Agropyron repens* (L.) Beauv., *Arenaria serpyllifolia* L., *Aster novae-angliae* L., *A. ericoides* L., *A. lateriflorus* (L.) Britton, *Chrysanthemum leucanthemum* L., *Diplotaxis tenuifolia* (L.) DC, *Erigeron canadensis* (L.), *Hypericum perforatum* L., *Medicago lupulina* L., *Phleum pratense* L., *Poa compressa* L., *Rumex crispus* L., *Silene vulgaris* (Moench) Garcke, *Solidago canadensis* L. All of these are species which are common in waste areas and old fields in southwestern Ontario (Alex and Switzer 1976, McKay and Catling 1979).

The species composition of the ruderal community which has developed on the study site can be expected to change over time. As perennial species such as *Agropyron repens* and *Solidago canadensis* expand clonally, it is expected that the percent cover within the community should increase, soil horizons should slowly develop, the water holding capacity of the substrate should increase, and the harshness of the microclimate should be ameliorated. Harper (1977), Grime (1979) and Silvertown (1982) have described similar processes for other ruderal communities. In all likelihood many, if not all, of the annual and biennial species which were present at the time of my study will eventually be excluded because their seeds require full sunlight to germinate and their seedlings cannot establish successfully in competition with established vegetation. Hart (1977), Harper (1977), Silvertown (1982) and

Fenner (1985) have described a similar fate for seeds and seedlings of other annual and biennial species. In nutrient poor areas with little or no soil development, however, such changes in a plant community often take place very slowly. Klemow (1982) found that 50 years after mining ceased at a limestone quarry in New York the plant community which had developed was still very patchy. He reported that some locations within the quarry had cover values of 100% whereas many other areas were completely barren. During the years since abandonment, the open habitat in the Marshall pit has supported several generations of the 15 biennial species included in my study. In all likelihood the vegetation in the study area will remain relatively open for years to come and this will allow the continued regeneration of populations of these biennial species.

Systematic surveys of the presence or absence of individuals of each of the 15 biennial species throughout the study area were made in 1981 and 1983. For each of these surveys the nine horizontal permanent transects previously established in the study area (see above) were augmented by the creation of 8 additional temporary horizontal transects which were located between the existing transects at 1.5m intervals. In sampling a 1.0 X 1.0m light-weight wooden quadrat was placed adjacent to the upper side of each horizontal transect at each consecutive 1.0m interval and the presence or absence of each of the 15 biennial species within that quadrat was recorded. The percent of quadrats which contained at least one individual of each species are presented for each survey in Table 2.2. I was not able to distinguish between *Melilotus alba* and *Melilotus officinalis* in the juvenile stage, so a category of *Melilotus* spp. is provided in the table to account

Species	1981 (n=1140)	1983 (n=1130)
Arctium minus	1.1	0.8
Cirsium vulgare	5.9	5.0
Daucus carota	88.1	93.9
Dipsacus sylvestris	1.4	2.5
Echium vulgare	17	17.5
Lactuca scariola	5.1	0.5
Melilotus alba	70.4	23.4
Melilotus officinalis	29.0	27.1
Melilotus spp.	80.5	84.9
Oenothera biennis	30.7	14.6
Onopordum acanthium	3.5	0.6
Tragopogon dubius	6.0	13.9
Verbascum blattaria	0.1	0.3
Verbascum thapsus	3.4	8.0

Table 2.2. Mean percent of 1.0m² quadrats which contained at least one individual of each biennial species during each of two census periods. The census was performed in July of each year.

for quadrats which contained a juvenile individual of one of both of these species. In both 1981 and 1983 *Daucus carota* and the two *Melilotus* species were by far the most numerous biennial species in the study area (Table 2.2). The percent occurrence of several of the biennial species changed between the two surveys. *Echium vulgare* nearly tripled, while *Dipsacus sylvestris*, *Tragopogon dubius*, and *Verbascum thapsus* doubled (Table 2.2). The percent occurrence of *Lactuca scariola* was reduced by 90%, that of *Onopordum acanthium* was reduced by approximately 80% and that of *Oenothera biennis* was halved (Table 2.2).

I thought that it was possible that the distribution of the 15 biennial species within the study area could be related to the distribution of macronutrients within the study area. To investigate this possibility I took the presence/absence data collected for each species in the 1981 survey (see above) and compared them with the levels of total phosphorus, potassium, and magnesium which were determined from substrate cores collected throughout the study area in 1981 as part of its physical characterization (see above). For each biennial species, a logistic regression was performed to determine whether or not the distribution of that species within the study area could be associated with the levels of one of more of these three nutrients (Sokal and Rohlf 1981). The procedure employed was FUNCAT from the Statistical Analysis System (SAS 1982). No significant ($P<0.05$) relationship was found between the distribution of any of the biennial species and the levels of any of these three nutrients within the study area.

Chapter 3

Seed Number, Seed Weight, and Seed Dispersal

3.1 Introduction

None of the 15 biennial species included in this investigation has the potential for vegetative propagation (*sensu* Silvertown 1982); each is entirely dependent on seed production for successful regeneration. Unless specifically noted otherwise, the word 'seed' is used throughout this thesis in a general sense (*sensu* Harper et al. 1970). According to this definition, a seed is the unit of the fertilized ovule and its associated structures, which is dispersed or sown. The seed plays several vital roles in the life cycle of these species. It is the means through which (1) a local population increases in size and by which individuals which die are replaced (Harper 1977, Cavers 1983); (2) new areas removed in space from the parent population are colonized and by which individuals survive unfavorable periods (Harper 1977, Cavers 1983); and (3) a species expresses genetic variation (Harper 1977, Cavers 1983). Before any of these roles can be filled however, a maturing seed must survive to ripen and disperse from the parent plant.

Seeds and fruits ripening on the parent plant present a quantity of discretely packaged resources which are normally of much higher nutritive quality than other plant parts (Fenner 1985). Accordingly, seeds are utilized by numerous predators. According to Janzen (1971), seed predators in their native habitats normally eat from 10 to 90% of the mature or nearly mature

seeds produced by species on which they feed. Plant species in turn employ a variety of mechanisms to minimize predispersal seed losses to predators. These include chemical and mechanical defenses in the infructescence, modification of the flowering period to escape the predator, reduction of flower size, and production of a large number of seeds (Fenner 1985). This latter strategy depends on the reproductive output of the plant being sufficient to satiate the local predators and yet have a proportion of the seeds survive to fulfill their vital functions (Harper 1977, Silvertown 1982, Fenner 1985).

From the perspective of a plant, the physical environment can be viewed as a matrix where seeds do not germinate and seedlings do not emerge and establish, interspersed with locations where seeds do germinate and seedlings do emerge and establish (Werner 1979, Fenner 1985). These locations which provide the species-specific conditions favorable for germination, emergence, and establishment have been termed 'safe sites' by Harper (1977). If a species produces a large number of seeds and effectively disperses a large proportion of them, the probability will be high that the safe sites specific for that species in that habitat will be filled (Cavers 1983).

Each plant species has a characteristic strategy for the allocation of resources to reproduction (Silvertown 1982, Harper 1977). Central to this strategy is the partitioning of seed production into a large number of small seeds or a smaller number of larger seeds (Harper et al. 1970, Stebbins 1971, Silvertown 1982, Fenner 1985). Small seeds are readily dispersed over a wide area (Salisbury 1942, Harper et al. 1970, Stebbins 1971, Stergios 1976, Harper 1977, Wilbur 1977, Silvertown 1982, Fenner 1985). Large seeds contain a large

embryo and/or a relatively large quantity of stored nutrients (Harper et al. 1970, Stebbins 1971, Harper 1977, Fenner 1983, Fenner 1985). As a result, a large seed produces a superior seedling which is able to rapidly develop an extensive root system and/or reach a critical shoot size, which in turn will allow it to compete successfully for resources with other plants (Salisbury 1942, Black 1958, Harper and Clatworthy 1963, Cavers and Harper 1966, Cavers and Harper 1967b, Harper et al. 1970, Stebbins 1971, Baker 1972, Weis 1982, Gross and Werner 1982, Fenner 1983, Gross 1984, Stanton 1984, Stanton 1985, Wulff 1986b). The mean weight per seed of a species is in all likelihood a compromise between the requirements for diaspore dispersal and the demands for seedling establishment (Salisbury 1942, Harper et al. 1970, Stebbins 1971, Harper 1977, Fenner 1985). Mean weight per seed is among the least phenotypically plastic characters of a plant (Salisbury 1942, Harper et al. 1970, Harper 1977, Silvertown 1982, Fenner 1985). According to Harper et al. (1970), lack of phenological plasticity in mean weight per seed is a homeostasis affecting the organ which is most important for maintaining the continuity between generations.

Ultimately, the regeneration of a species which has no clonal growth is dependent upon its seeds reaching safe sites. The diaspores of plant species are dispersed by a myriad of vectors, some of which are highly specific in their actions (Ridley 1930, van der Pijl 1982, Howe and Smallwood 1982). Diaspores of species which colonize drastically disturbed sites such as glacial moraines and abandoned open pit mines and quarries, however, tend to be either transported by wind, externally by animals, or are small-seeded species which have no obvious adaptation for dispersal (Croxton 1928,

Bramble and Ashley 1955, Schramm 1966, Viereck 1966, Byrnes and Miller 1973, Heagy 1981).

In this chapter the portions of the life cycles of the 15 biennial species beginning with seed set and continuing through dispersal were investigated. The mean reproductive output of each of the 15 biennials after predation was estimated; the mean weight per seed of each of the biennials was calculated; and the potential for diaspores of the biennials to be dispersed by wind, water, and external animal transport was assessed.

3.2 Materials and Methods

A. Plant height

During the 1981 and 1982 growing seasons, the mean maximum height of the flowering stalk was determined for each of the fifteen biennial species. For each species an attempt was made to mark 100 flowering individuals with tags numbered sequentially from 1 through 100 within the Marshall pit. If, however, for any given species fewer than 100 flowering individuals were present in the Marshall pit, additional flowering individuals were tagged in the West Nissouri and Hill pits (within 3km of the Marshall pit, for further detail see Heagy 1981) until either 100 or the maximum number of flowering individuals present were marked. For each species in which 100 flowering individuals had been tagged, 25 random numbers from 1 through 100 were generated and the flowering individuals with numbered tags which corresponded to one of the 25 random numbers were measured. For each species in which more than 25 but fewer than 100 flowering individuals had

been tagged, 25 random numbers were generated from 1 through the number of individuals present and the flowering individuals with numbered tags which corresponded to one of the 25 random numbers were measured. For each species in which fewer than 25 flowering individuals had been tagged, every flowering individual was measured. For each species every flowering individual selected for measurement was measured along the stalk from the ground to the highest point and the number of either fruits or infructescences, whichever was appropriate for the architecture of that species, was recorded.

B. Reproductive output

During the 1981 and 1982 growing seasons, the mean net reproductive output was estimated for each species as follows. First, the mean number of either fruits or infructescences per flowering plant was estimated. Then the mean number of seeds per fruit or infructescence was multiplied by the mean number of fruits or infructescences per flowering plant to estimate the mean gross reproductive output per plant of a species. Finally, the mean number of seeds destroyed by predators was estimated. The potential mean net seed production per plant for each species was then estimated by subtracting the mean number of seeds destroyed by predators from the mean gross reproductive output. However, variations among the biennial species in both phenology and architecture required that this general procedure be modified according to the characteristics of each particular species.

The entire seed crop of *Alliaria petiolata* ripened approximately simultaneously and ripened seeds were retained within the fruit until all

seeds were mature. For this species the 25 flowering individuals selected for measurement of plant height were collected entire, seeds were separated from the fruits, and the number of seeds produced by each plant was counted.

For the remaining species however, the seed crop matured over a period of weeks and so it was logistically impractical to count every seed produced by 25 individuals of each species. Sampling procedures were developed which took into account the individual abundance, phenology and architecture of these species. For each of these species however, the mean number of fruits or infructescences per flowering individual was estimated by counting the number of fruits or infructescences which were present on each of the 25 flowering individuals which were selected randomly for height measurement.

For each of eight species, *Arctium minus*, *Cirsium vulgare*, *Daucus carota*, *Echium vulgare*, *Melilotus alba*, *Melilotus officinalis*, *Onopordum acanthium* and *Tragopogon dubius*, 1000 infructescences were marked with tags numbered sequentially from 1 through 1000 and 100 random numbers were generated from 1 through 1000. Every infructescence with a numbered tag corresponding to one of the random numbers was collected, the number of seeds per infructescence was counted, and the number of seeds per infructescence destroyed by predators was estimated.

An identical sampling procedure was employed for *Lactuca scariola* and *Tragopogon pratensis*. There were, however, fewer individuals of these two species available for sampling. For *Lactuca scariola* only 6 individuals and 90 infructescences were available. For *Tragopogon pratensis* only 3

individuals were available in the gravel pits and it was not possible to determine the number of seeds per infructescence in any of those three individuals because many seeds had been dispersed before these plants were located.

For both *Oenothera biennis* and *Verbascum thapsus*, 1000 fruits were marked with tags sequentially numbered from 1 through 1000 and 100 random numbers were generated from 1 through 1000. Every fruit with a numbered tag which corresponded to one of the random numbers was collected, the number of seeds per fruit was counted, and the numbers of seeds per fruit which had been destroyed by predators were determined. An identical sampling procedure was employed for *Verbascum blattaria*. There were, however, only 50 fruits available for estimation of the number of seeds per fruit in this latter species.

The number of seeds per infructescence of *Dipsacus sylvestris* was estimated mathematically in the manner of Werner (1975a). According to Werner (1975a), each involucral bract in the infructescence of *Dipsacus sylvestris* supports one ovule. The number of seeds per infructescence in this species varies directly with the size of the infructescence, and the size of the infructescence can be estimated by the length of the rachis which forms the core of the infructescence (Werner 1975a). I selected ten *Dipsacus sylvestris* infructescences at random. For each, I counted the involucral bracts and measured the length of the rachis. The number of seeds per infructescence could then be determined from the experimentally derived equation $Y = 238.4X + 84.9$, where X = the length of the rachis and Y = the number of involucral bracts. One thousand infructescences of

Dipsacus sylvestris were then marked with numbered tags and 100 random numbers were generated from 1 through 1000. All infructescences which had been tagged with a number which corresponded to one of the random numbers were collected, the length of the rachis was measured and the number of ovules estimated according to the preceding formula. According to Werner (1975a) approximately 80% of the ovules are actually fertilized. The estimated mean number of ovules per flowering individuals was multiplied by 0.8 to approximate the number of viable seeds produced.

Infructescences of *Cirsium vulgare*, *Lactuca scariola*, *Onopordum acanthium*, *Tragopogon dubius* and *Tragopogon pratensis* were observed to have been predated by American goldfinches (*Carduelis tristis* L.) (henceforth called goldfinches). A given goldfinch did not destroy all the seeds in an infructescence which it attacked; a portion was eaten, but a portion was scattered unharmed by the activity of the feeding bird. For the purposes of this investigation it was estimated that 30% of the seeds in an infructescence of one of these species which had been attacked by goldfinches were actually destroyed (estimate based on information from W.G. Stewart, personal communication) and the estimated mean gross reproductive output for each of these species was adjusted accordingly.

C. Seed weight

In 1983 the mean weight of seeds of each of the 15 biennial species was determined at several times during the fruiting period. In this section of this chapter, the word 'seed' is used in a very specific sense to refer to the product of a ripened ovule. For each species the general seed

collection procedures were as follows. Because of logistical constraints I selected a group (group size was always more than 10 individuals) of fruiting plants which were growing in general physical proximity to one another in either the Marshall, Hill, or West Missouri pits. A bulk sample of all seeds or fruits (as appropriate) which were ripe and readily dispersable was collected from each of the plants in the group sampled. In some species the location of the fruit in the infructescence has been shown to be strongly correlated with seed size (Cavers and Harper 1966, Maun and Cavers 1971). Great care was taken on every sampling date to collect ripe seeds representatively from all parts of the infructescence of each individual sampled to obviate any such a position effect.

The seeds of each species were collected in a manner appropriate to the architecture of that particular species. Individual fruits of *Cirsium vulgare*, *Lactuca scariola*, *Onopordum acanthium*, *Tragopogon dubius*, and *Tragopogon pratensis* were collected by hand when ripe, taken to the laboratory and the pappus removed by hand. Entire umbels of *Daucus carota* and individual fruits of *Alliaria petiolata*, *Arctium minus*, *Echium vulgare*, *Melilotus alba*, and *Melilotus officinalis* were stripped from the infructescence by hand and brought back to the laboratory where the fruits or infructescences were ruptured mechanically to release the seeds. The resultant material was then passed through a nest of soil sieves with graded mesh sizes and seeds were separated from the residue by means of a commercial seed blower. For *Dipsacus sylvestris*, *Oenothera biennis*, *Verbascum blattaria*, and *Verbascum thapsus* the infructescences were shaken gently to release mature seeds into a large paper bag, but not shaken

so vigorously that unripe seeds were dislodged.

The seed crop of *Alliaria petiolata* matured approximately simultaneously, so only one sample was collected from this species. Only one sample was collected for *Tragopogon pratensis* as well. Only 3 flowering *Tragopogon pratensis* individuals were present in the Marshall, West Nissouri and Hill pits, so a collection was made from individuals growing along roadsides within the city of London. The city government pursued an aggressive weed control program that summer however, and all roadsides were mown soon after the initial *Tragopogon pratensis* collection, making subsequent collections impossible. Two collections were made for *Tragopogon dubius*, one early and one late in the fruiting period. For each of the remaining species, three collections were made, one early, one intermediate, and one late in the fruiting period. Since the length of the fruiting period varied according to the phenology of each individual species, the three sampling dates were not consistent chronologically, but were selected arbitrarily at times appropriate to each species. Once collected, fruits from each species were stored in dry paper bags at ambient temperatures until seeds could be processed.

Once the seed collection from a given species on a given sampling date had been cleaned, the seeds were thoroughly mixed and a subsample of 50 was randomly selected. Each of the 50 seeds in the subsample was stored in a separate paper coin envelope at room temperature until all seed collections from all species had been processed. Immediately prior to weighing, all seed-containing coin envelopes were placed in a desicoator for 24 hours. All seeds were weighed individually on a Cahn 25 automatic

electrobalance. Mean seed weight was determined for each sampling date for each species. For each species which was sampled on more than one sampling date, mean weights per seed were compared statistically between sampling dates to determine whether or not seed weight varied significantly across the growing season. Before any statistical analysis was performed, all seed weights were transformed to natural logarithm values to normalize the variance (Sokal and Rohlf 1981). Since there were only 2 sampling dates for *Tragopogon dubius* a Student's t-test was performed to compare the two means. In the remaining species a one-way ANOVA was performed to compare the three means.

D. Dispersal

In 1983 the potential of diaspores of the 15 biennial species to be dispersed by wind, water and external animal transport was assessed. For each species, all diaspores which were used in these tests of dispersability were collected as they became ripe in the field. Diaspores of species whose diaspore included a pappus, *Cirsium vulgare*, *Lactuca scariola*, *Onopordum acanthium*, *Tragopogon dubius* and *Tragopogon pratensis* were collected by hand and stored in glass jars to protect them from damage. The burs of *Arctium minus* and the indehiscent pods of *Melilotus alba* and *Melilotus officinalis* were collected by hand and were stored in dry paper bags. Fruits of *Alliaria petiolata*, *Daucus carota*, *Dipsacus sylvestris*, *Echium vulgare*, *Oenothera biennis*, *Verbascum blattaria* and *Verbascum thapsus* were collected and processed to liberate the seeds. For *Daucus carota*, *Dipsacus sylvestris* and *Echium vulgare* infructescences were pulled apart by hand

whereas for *Alliaria petiolata*, *Oenothera biennis*, *Verbascum blattaria* and *Verbascum thapsus* fruits were mechanically ruptured to release seeds. For all these species the resultant material was passed through a nest of soil sieves with graded mesh sizes. Seeds were then separated from the residue of fruits or infructescences by means of a commercial seed blower. Once separated, seeds were stored in glass jars.

The potential of diaspores of the 15 biennials to be transported by wind was assessed in the field in 1983. A circle of nylon cloth of 1m radius was cut and concentric rings spaced at 0.25m intervals were drawn on it. In determining the dispersability by wind of diaspores of each species, the nylon circle was placed in an open area in the field on three separate dates and fifty newly ripened diaspores were dropped from mean plant height at the center of the circle on each date. The distance the diaspores fell from the drop point was recorded in 0.25m increments. On each sampling date a variable breeze was blowing, but no sampling date had winds strong enough to register on a hand-held anemometer. For each species the mean percent of diaspores which landed within each 0.25m incremental distance from the center drop point on each of the three sampling dates was calculated.

In 1983 the buoyancy of diaspores of the 15 biennial species was tested both in calm and in agitated distilled water in the laboratory. Fifty diaspores from each species were dropped from approximately mean plant height into 1L beakers three-quarters full of distilled water, one species to a beaker. The number of propagules which floated initially and the number which remained floating in undisturbed water after 24hr were recorded. This

procedure was repeated 3 times for each species with different sets of diaspores. The mean percent of propagules initially floating and the mean percent floating after 24hr were calculated for each species.

To test buoyancy under agitated conditions fifty diaspores from each species were again dropped from approximately mean plant height into 500 mL glass jars three-quarter full of distilled water, one species to a jar. The number of diaspores which floated initially was recorded. The jars were then tightly capped and placed on a mechanical agitator where they were shaken for 15 minutes at low speed. When the jars were removed from the agitator, the number of diaspores which were floating was recorded immediately. The jars were then allowed to stand for 15min and the number of diaspores which were floating was recorded. This procedure was repeated 3 times with different sets of diaspores for each species. For each species the mean percent of diaspores floating at each time of recording was calculated.

A groundhog (*Marmota monax* L.) was killed, skinned, and its pelt stretched over a 2 l plastic fruit juice container to roughly approximate the body shape of the animal. This pelt was then used to assess the potential of diaspores of the 15 biennials to be carried in animal fur. For each species 50 diaspores were spread evenly on a lab bench, the pelt was dragged through them, and the number of diaspores picked up by the pelt was counted. Then 50 more diaspores were spread evenly on the lab bench and the pelt was dragged through again, this time however, it was agitated vigorously during the drag in an attempt to simulate the locomotion of the living groundhog. The number of diaspores picked up by the pelt was then counted. This

procedure was repeated 3 times for each species. Then the procedure was repeated 3 times for each species after the groundhog pelt had been sprayed with water to make it wet. The mean percent of diaspores of each species which were picked up by the groundhog pelt at each time of recording was then calculated.

3.3 Results

A. Plant height

The mean heights of the flowering stalks of the biennial species are presented in Table 3.1. The heights ranged from a low of 45.4cm in *Oenothera biennis* to a high of 133.3cm in *Melilotus alba*. The flowering stalks of all species were relatively large and coarse when compared with the growth forms of other species in the community.

B. Reproductive output

The estimated mean reproductive outputs of the biennial species both before and after predation are presented in Table 3.2. The potential number of seeds which survived to disperse was highly variable, ranging from 119 in *Tragopogon dubius* to 22,425 in *Verbascum thapsus*.

In several species potential reproductive output was reduced by the activities of seed predators. It was estimated that approximately 30% of the seeds produced in capitula of *Cirsium vulgare*, *Lactuca scariola*, *Onopordum acanthium* and *Tragopogon dubius* were destroyed by goldfinches. In addition, for *Onopordum acanthium* nearly 2.0% of the

Species	Mean Plant Height (cm)
Alliaria petiolata	91.0 ± 16.8
Arctium minus	120.7 ± 32.4
Cirsium vulgare	110.7 ± 33.5
Daucus carota	82.1 ± 24.8
Dipsacus sylvestris	123.4 ± 35.6
Echium vulgare	46.1 ± 18.0
Lactuca scariola	95.7 ± 53.7(n = 6)
Melilotus alba	133.3 ± 36.2
Melilotus officinalis	100.0 ± 28.6
Oenothera biennis	45.4 ± 13.8
Onopordum acanthium	125.6 ± 44.1
Tragopogon dubius	52.8 ± 14.3
Tragopogon pratensis	71.3 ± 42.4(n = 3)
Verbascum blattaria	89.2 ± 31.8
Verbascum thapsus	121.9 ± 39.4

Table 3.1. Mean height (± S.D.) of flowering plants of each of 15 biennial species which occurred in the Marshall pit (n = 25 unless otherwise noted).

Species	Estimated Reproductive output before predation	after predation
Alliaria petiolata	618	618
Arctium minus	14,643	3,851
Cirsium vulgare	13,236	9,266
Daucus carota	972	972
Dipsacus sylvestris	2,477	2,477
Echium vulgare	4,726	4,726
Lactuca scariola	2,845	2,751
Melilotus alba	9,712	9,712
Melilotus officinalis	5,165	5,165
Oenothera biennis	2,067	2,067
Onopordum acanthium	2,902	2,391
Tragopogon dubius	124	119
Verbascum blattaria	7,653	7,500
Verbascum thapsus	38,008	22,425

Table 3.2. Estimated numbers of seeds produced by 14 biennial species in the Marshall pit both before and after pre-dispersal predation (see text for details of methods employed).

capitula sampled were destroyed by the stem-boring larvae of the lepidopteran *Papaipema nebris* Guenee. Thirty-five percent of the capsules of *Verbascum thapsus* and 2.0% of those of *Verbascum blattaria* had all their seeds destroyed by larvae of the cuculionid weevil *Gymnaetron tetrum* Fab. Approximately 74% of the seeds produced by flowering *Arctium minus* plants sampled in this study were destroyed by larvae of the burdock moth, *Metzneria lappella* Zeller.

C. Seed weight

The mean weights of the seeds of the 15 biennial species sampled on up to three dates during their respective fruiting periods are presented in Table 3.3. Species are listed in the table according to decreasing mean weight per seed. Gross (1984) artificially divided the 6 biennials in her study into large, intermediate and small seeded species on the basis of mean weight per seed. Following her convention, the biennials in this study can be grouped as relatively large seeded: *Onopordum acanthium*, *Tragopogon pratensis*, *Arctium minus* and *Tragopogon dubius*; intermediate: *Echium vulgare*, *Melilotus alba*, *Melilotus officinalis*, *Dipsacus sylvestris*, *Alliaria petiolata*, *Cirsium vulgare*, *Daucus carota* and *Lactuca scariola*; and relatively small seeded: *Oenothera biennis*, *Verbascum blattaria* and *Verbascum thapsus*.

The mean weights per seed varied from 0.07mg for *Verbascum thapsus* to 13.03mg for *Onopordum acanthium*. Six biennials had a statistically significant difference ($P<0.05$) in mean weight per seed between sampling dates. Two of these species, *Echium vulgare* and *Cirsium vulgare*, had overall

Species	Date 1	Date 2	Date 3	
Onopordum acanthium	11.27 ± 3.10	13.03 ± 2.71	12.06 ± 2.59	ns
Tragopogon pratensis	8.65 ± 2.23	---	---	
Arctium minus	5.62 ± 1.65	8.29 ± 2.22	6.78 ± 1.54	***
Tragopogon dubius	5.35 ± 1.35	---	6.60 ± 2.18	***
Echium vulgare	2.66 ± 0.43	2.62 ± 0.42	2.57 ± 0.48	*
Melilotus alba	1.97 ± 0.40	2.06 ± 0.37	2.02 ± 0.31	ns
Melilotus officinalis	2.01 ± 0.54	2.01 ± 0.38	1.81 ± 0.39	ns
Dipsacus sylvestris	2.02 ± 0.40	1.96 ± 0.30	1.91 ± 0.42	ns
Alliaria petiolata	1.65 ± 0.28	---	---	
Cirsium vulgare	1.71 ± 0.70	1.40 ± 0.42	1.36 ± 0.42	*
Daucus carota	0.74 ± 0.20	0.75 ± 0.24	0.75 ± 0.15	ns
Lactuca scariola	0.61 ± 0.11	0.64 ± 0.06	0.75 ± 0.14	***
Oenothera biennis	0.34 ± 0.09	0.53 ± 0.24	0.72 ± 0.19	***
Verbascum blattaria	0.12 ± 0.03	0.12 ± 0.02	0.12 ± 0.02	ns
Verbascum thapsus	0.07 ± 0.02	0.07 ± 0.02	0.07 ± 0.02	ns

*** = significant at P<0.001
* = significant at P<0.05
ns = not significant

Table 3.3. Mean (± S.D.) weight per seed (in mg) of seeds of 15 biennial species collected on three dates in the Marshall pit (n = 50). See text for explanation where fewer than 3 collections were made. Significance levels refer to within-species differences between means on different dates.

decreases in mean weight per seed as the growing season progressed, *Tragopogon dubius*, *Lactuca scariola* and *Oenothera biennis* had overall increases in mean weight per seed as the growing season progressed, and *Arctium minus* had the greatest mean weight per seed at the intermediate date

D. Dispersal

The mean percent of diaspores of each of the biennial species which were dispersed by wind to each of 5 distance categories (*ie.* 4 incremental distances up to 1m and beyond 1m) are presented in Table 3.4. The biennials fell into two groups on the basis of the potential of their diaspores to be dispersed by wind. Diaspores of four species whose diaspores included a pappus as well as the two lightest seeded species were carried furthest by the wind. More than 70% of the diaspores of *Cirsium vulgare*, *Lactuca scariola*, *Tragopogon dubius*, *Tragopogon pratensis*, *Verbascum blattaria* and *Verbascum thapsus* travelled at least 0.75m from the drop point. More than 70% of the diaspores of the remaining species travelled less than 0.5m, except for those of *Daucus carota*, 66% of which travelled less than 0.5m and 33% of which travelled more than 1m from the drop point.

All of these biennial species have the potential to have their diaspores transported by calm water for at least 24hr. Only two species failed to have 100% of their diaspores remain floating for 24hr in distilled water. Of these two species, 100% of the diaspores of *Verbascum thapsus* floated initially, but only 99.3% remained floating after 24 hr. whereas 98.7% of the diaspores of *Echium vulgare* floated initially, all of which remained

Species	0–25 cm	25–50 cm	50–75 cm	75–100 cm	>100 cm
Alliaria petiolata	84.3 ± 43.6	15.3 ± 21.4	0.7 ± 1.2	0.0 ± 0.0	0.0 ± 0.0
Arctium minus	92.7 ± 12.7	4.0 ± 6.9	3.3 ± 5.8	0.0 ± 0.0	0.0 ± 0.0
Cirsium vulgare	0.0 ± 0.0	2.0 ± 3.5	8.7 ± 9.0	6.0 ± 6.0	83.3 ± 14.5
Daucus carota	63.3 ± 55.1	3.3 ± 5.8	0.0 ± 0.0	0.0 ± 0.0	33.3 ± 57.7
Dipsacus sylvestris	84.0 ± 27.7	3.3 ± 5.8	6.7 ± 11.5	3.3 ± 5.8	1.3 ± 2.3
Echium vulgare	93.3 ± 4.6	6.7 ± 4.6	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Lactuca scariola	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	100.0 ± 0.0
Melilotus alba	65.3 ± 54.8	4.7 ± 3.0	8.7 ± 15.0	6.0 ± 10.4	15.3 ± 26.6
Melilotus officinalis	64.7 ± 49.6	7.3 ± 7.0	7.3 ± 12.7	7.3 ± 12.7	13.3 ± 23.1
Oenothera biennis	87.3 ± 8.1	12.7 ± 8.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Onopordum acanthium	62.7 ± 42.1	11.3 ± 3.0	7.3 ± 6.4	9.3 ± 8.3	21.3 ± 27.2
Tragopogon dubius	2.0 ± 0.0	8.0 ± 5.3	12.7 ± 15.0	12.7 ± 9.9	64.7 ± 11.4
Tragopogon pratensis	3.3 ± 2.3	12.7 ± 8.3	11.3 ± 6.1	18.7 ± 3.0	54.0 ± 15.9
Verbascum blattaria	0.0 ± 0.0	0.0 ± 0.0	4.7 ± 8.1	20.7 ± 26.1	74.6 ± 34.0
Verbascum thapsus	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	100.0 ± 0.0

Table 3.4. Mean percentage of diaspores (± S.D.) in each of five distance categories for 15 biennial species dropped from mean plant height in the field on 3 sampling dates (N = 150).

floating after 24 hr. These data conflict with the pre-agitation results from a separate experiment which are presented in Table 3.5.

The mean percent of diaspores of the biennial species which floated initially, which remained floating after 15 minutes agitation, and which remained floating after 15 additional minutes of settling are presented in Table 3.5. Thirteen of the biennial species have the potential to have their diaspores transported by turbulent water. All diaspores of every species except three floated initially. Of these three species, 96.7% of *Melilotus officinalis*, 50% of *Echium vulgare*, and 25% of *Alliaria petiolata* diaspores floated when they were first placed in the water. Seven species, *Arctium minus*, *Cirsium vulgare*, *Dipsacus sylvestris*, *Oenothera biennis*, *Tragopogon dubius*, *Tragopogon pratensis*, and *Verbascum thapsus* had more than 90% of their diaspores floating after 15 minutes agitation. *Melilotus alba*, *Melilotus officinalis*, and *Onopordum acanthium* had from 50 to 60% of their diaspores floating after 15 minutes agitation. *Daucus carota*, *Echium vulgare*, and *Lactuca scariola* had from 10 to 25% of their diaspores floating after 15 minutes agitation. *Verbascum blattaria* and *Alliaria petiolata* had less than 2% of their diaspores floating after 15 minutes agitation. The number of diaspores which were floating after the agitated water had settled for 15 minutes changed for *Dipsacus sylvestris*, *Onopordum acanthium*, and *Lactuca scariola* only. All three of these species had additional diaspores sink during the settling period: 3% for *Lactuca scariola*, 6% for *Dipsacus sylvestris* and 10% for *Onopordum acanthium*.

The mean percent of diaspores of the biennial species which clung to the fur of the groundhog pelt when it was dry and when it was wet are

Species	Floating initially	Agitated 15min	15min calm post-agitation
Alliaria petiolata	25.3 ± 8.3	0.0 ± 0.0	0.0 ± 0.0
Arctium minus	100.0 ± 0.0	100.0 ± 0.0	100.0 ± 0.0
Cirsium vulgare	100.0 ± 0.0	100.0 ± 0.0	100.0 ± 0.0
Daucus carota	100.0 ± 0.0	15.3 ± 4.2	15.3 ± 5.8
Dipsacus sylvestris	100.0 ± 0.0	92.7 ± 7.0	86.7 ± 12.2
Echium vulgare	50.0 ± 2.0	10.0 ± 12.5	10.6 ± 9.9
Lactuca scariola	100.0 ± 0.0	22.0 ± 0.0	19.3 ± 3.0
Melilotus alba	100.0 ± 0.0	53.3 ± 14.7	51.3 ± 16.0
Melilotus officinalis	96.7 ± 3.0	50.0 ± 2.0	51.3 ± 4.2
Oenothera biennis	100.0 ± 0.0	97.3 ± 3.0	97.3 ± 3.0
Onopordum acanthium	100.0 ± 0.0	64.7 ± 4.2	54.8 ± 15.3
Tragopogon dubius	100.0 ± 0.0	100.0 ± 0.0	100.0 ± 0.0
Tragopogon pratensis	100.0 ± 0.0	100.0 ± 0.0	100.0 ± 0.0
Verbascum blattaria	100.0 ± 0.0	1.3 ± 1.2	1.3 ± 1.2
Verbascum thapsus	100.0 ± 0.0	100.0 ± 0.0	100.0 ± 0.0

Table 3.5. Mean percent of diaspores (± S.D.) of 15 biennial species which floated in distilled water initially, were floating after 15min agitation, and were floating after 15min post-agitation calm (n = 150). See text for an explanation of methods employed.

presented in Table 3.6. All of the biennial species can have their diaspores transported at least for short distances within dry animal pelts. More than 60% of the diaspores of *Arctium minus*, *Daucus carota*, and *Lactuca scariola* were picked up by the dry pelt on both the straight and the agitated passes. Four species, *Dipsacus sylvestris*, *Oenothera biennis*, *Verbascum blattaria*, and *Verbascum thapsus* had fewer than 6% of their diaspores picked up by the dry pelt on either the straight or the agitated pass. The remaining 8 species had from 7 to 70% of their diaspores picked up by the pelt on one or both of the straight and agitated passes.

All of the biennial species can have their diaspores transported, at least for short distances, within the wet pelts of animals. More than 65% of the diaspores of *Alliaria petiolata*, *Arctium minus*, *Daucus carota*, *Dipsacus sylvestris*, *Lactuca scariola*, *Melilotus alba*, *Melilotus officinalis*, *Oenothera biennis*, *Verbascum blattaria*, and *Verbascum thapsus*; from 50 to 75% of those of *Echium vulgare* and *Onopordum acanthium*; and approximately 25% of those of *Cirsium vulgare* were picked up by the wet pelt on both the straight and agitated passes (Table 3.6). In contrast, less than 6% of the diaspores of either *Tragopogon dubius* or *Tragopogon pratensis* were picked up by the wet pelt on either the straight or agitated pass.

Greater numbers of diaspores of nine species, *Alliaria petiolata*, *Dipsacus sylvestris*, *Echium vulgare*, *Melilotus alba*, *Melilotus officinalis*, *Oenothera biennis*, *Verbascum blattaria*, and *Verbascum thapsus* clung to the groundhog pelt when it was wet (Table 3.6). Both *Tragopogon* species however, had greater numbers of diaspores picked up by the pelt when it

	Dry		Wet	
Species	Straight	Agitated	Straight	Agitated
Alliaria petiolata	1.3 ± 1.2	6.0 ± 5.3	97.3 ± 3.0	93.3 ± 4.2
Arctium minus	71.3 ± 4.2	92.0 ± 6.0	78.7 ± 9.5	98.7 ± 1.2
Cirsium vulgare	8.0 ± 2.0	32.7 ± 15.0	24.0 ± 14.0	28.0 ± 2.0
Daucus carota	67.3 ± 6.4	60.7 ± 12.2	65.7 ± 49.1	98.0 ± 3.5
Dipsacus sylvestris	0.0 ± 0.0	2.7 ± 1.2	99.3 ± 1.2	90.0 ± 11.1
Echium vulgare	8.0 ± 4.0	7.3 ± 3.0	62.7 ± 23.9	78.7 ± 12.0
Lactuca scariola	70.7 ± 11.0	81.3 ± 8.3	72.7 ± 24.7	96.7 ± 5.8
Melilotus alba	12.0 ± 4.0	6.7 ± 1.2	86.7 ± 3.0	90.0 ± 10.6
Melilotus officinalis	17.3 ± 5.0	14.0 ± 2.0	93.3 ± 4.2	78.0 ± 12.5
Oenothera biennis	2.3 ± 1.5	4.7 ± 4.6	97.3 ± 4.2	89.3 ± 6.4
Onopordum acanthium	6.7 ± 2.3	16.0 ± 5.3	72.0 ± 9.2	56.0 ± 14.4
Tragopogon dubius	9.3 ± 6.1	23.3 ± 1.2	2.0 ± 0.0	5.3 ± 4.2
Tragopogon pratensis	17.3 ± 8.3	22.0 ± 9.2	2.7 ± 1.2	3.3 ± 1.2
Verbascum blattaria	2.0 ± 2.0	.07 ± 1.2	95.3 ± 3.0	92.0 ± 2.0
Verbascum thapsus	4.0 ± 0.0	1.3 ± 1.2	97.3 ± 1.2	96.7 ± 1.2

Table 3.6. Mean percent (± S.D.) of diaspores of 15 biennial species which adhered to a wet or dry *Marmota monax* pelt when it was passed through them (n = 150). See text for explanation of methods employed.

was dry (Table 3.6). The remaining 4 species, *Arctium minus*, *Cirsium vulgare*, *Daucus carota*, and *Lactuca scariola*, had approximately similar numbers of diaspores picked up by the pelt both when it was wet and when it was dry (Table 3.6).

3.4 Discussion

A. Reproductive output

Biennials have often been described as species which produce large numbers of seeds, the hypothesis being that a large reproductive output is necessary for such species to achieve a rate of population increase comparable to that of annual and perennial species (Harper 1967, Schaffer and Gadgil 1975, Hart 1977, Harper 1977, Gross 1980a , Silvertown 1983, Thompson 1984, Kelly 1985b, de Jong and Klinkhammer 1986). Apparently, biennials are able to produce such large numbers of seeds through disproportionate allocation of resources to seed production. Some biennial species of the Umbelliferae were found to contribute proportionally eight times more resources to seed production than were contributed to seed production by perennial species in the same family (Louvett-Doust 1980). The theory that biennial species produce unusually large numbers of seeds was supported by the work of both Salisbury (1942), who reported that in the British flora, the mean number of seeds produced by herbaceous annuals, biennials, and perennials was 6,368, 28,790, and 5,869 respectively and Stevens (1932), who found that among North American weeds, biennials produced an average of 85,500 seeds per plant whereas annuals and perennials produced 20,832 and 16,629 seeds per plant respectively.

1. Reports from published studies

Records exist for the mean number of seeds produced by 13 of the biennial species included in this study. *Arctium minus* has been reported to produce from 11,600 to 31,600 seeds per plant in old fields and floodplains in southwestern Ontario and southern Michigan (Stevens 1932, Reed and Stephenson 1972, Hawthorn and Hayne 1978, Gross et al. 1980). *Cirsium vulgare* was found to produce from 50 to 5,000 seeds in sand dune systems in the Netherlands and 8,000 seeds per plant in a relatively nutrient rich garden in the Netherlands (van Leeuwen and van Breeman 1980, de Jong and Klinkhammer 1986), whereas Salisbury (1961) noted that 4,000 seeds per plant were produced by this species in Britain. *Daucus carota* has been reported as producing from 1,000 to 40,000 seeds per plant in southwestern Ontario and southern Michigan (Dale 1974, Gross and Werner 1982). Salisbury (1942) recorded seed production of 2,960 ± 495 seeds per plant for *Dipsacus sylvestris* in Britain, whereas Werner (1975a) estimated that 3,333 seeds per plant were produced by this species in old fields in southern Michigan. *Echium vulgare* was reported to produce 247 ± 35 seeds per plant in sparsely vegetated sites and 202 ± 21 to 303 seeds per plant in densely vegetated sites in an abandoned limestone quarry in New York (Klemow and Raynal 1985) and from 1000 to 10,000 seeds per plant in a dune system in the Netherlands (van Leeuwen and van Breeman 1980). Marks and Prince (1981) noted that *Lactuca scariola* produced a mean of 904 seeds per plant in Britain and Stevens (1932) reported that this species produced 27,900 seeds per plant in North Dakota. Turkington et al. (1978) found that openly grown plants of *Melilotus alba* produced from 200,000 to 350,000 seeds per plant

in southwestern Ontario. Stevens (1932) recorded a mean production of 14,235 seeds per plant for *Melilotus alba* in North America, and Klemow and Raynal (1981) reported that this species produced 9,710 seeds per plant in densely vegetated sites and 3,530 seeds per plant in sparsely vegetated sites in an abandoned limestone quarry in New York. Turkington et al. (1978) found that open grown plants of *Melilotus officinalis* produced 100,000 seeds per plant in southwestern Ontario. *Oenothera biennis* has been reported to produce from 25,200 to 33,000 seeds per plant in Britain (Ridley 1930, Salisbury 1961), whereas Stevens (1932) recorded production of 118,500 seeds per plant in North Dakota, and Gross and Werner (1982) found that 6,000 seeds per plant were produced by this species in old fields in southern Michigan. Young and Evans (1969) noted that plants of *Onopordum acanthium* grown in a garden in Nevada produced an average of 24,071 ± 13,602 seeds per plant. *Tragopogon dubius* was reported to produce a mean of 90 to 250 seeds per plant in in old fields in southern Michigan (Gross 1980a) and 450 seeds seeds per plant in North Dakota (Stevens 1957). *Verbascum thapsus* has been found to produce from 100,000 to 180,000 seeds per plant in old fields in southern Michigan (Gross and Werner 1978, Gross and Werner 1982, Gross 1980b). Stevens (1932) reported that there were 223,200 seeds per plant produced by this species in North Dakota, and Salisbury (1942) recorded mean seed production of 136,000 ± 32,000 for *Verbascum thapsus* in Britain.

The overall mean estimated potential reproductive output before predation of the 15 biennials in this study was 7,511 ± 2,646 seeds per plant; roughly one-quarter of that reported for the British biennials by Salisbury (1942) and less than ten percent of that recorded for North American

biennials by Stevens (1932). The mean numbers of seeds produced per plant in this study estimated for *Daucus carota*, *Dipsacus sylvestris*, *Melilotus alba*, *Melilotus officinalis*, *Oenothera biennis*, *Onopordum acanthium* and *Verbascum thapsus* are lower, in some cases substantially so, than the reproductive outputs reported for these species in the literature. The reproductive outputs estimated for *Arctium minus*, *Echium vulgare*, *Lactuca scariola*, and *Tragopogon dubius* are within the reported values, but occur on the lower end of the range. These low values are not unexpected since it has been shown for most species that mean seed size is a very constant character and that when growing in a situation of low resources, most plant species adjust their reproductive output through reduction in the number of inflorescences, hence number of seeds produced rather than in reduction of seed size (Salisbury 1942, Harper et al. 1970, Harper 1977, Silvertown 1982, Fenner 1985). The Marshall pit is a nutrient-poor environment (2.2 D). Plants growing there would be expected to produce fewer seeds than those growing in more nutrient-rich habitats such as gardens, old fields, and woods edges. Klemow and Raynal (1981, 1985) studied the population biology of *Melilotus alba* and *Echium vulgare* in a nutrient-poor limestone quarry. The values for reproductive output found for those species in the current study were equivalent to, or greater, than, those found by Klemow and Raynal (1981, 1985) in their quarry. The reproductive output of *Cirsium vulgare* is much greater in this study than that reported in the literature. The reported values however, both are from European studies. *Cirsium vulgare* is a relatively late flowering species (2.2) and perhaps the longer growing season in southwestern Ontario allowed it to produce more capitula and hence more seeds. This idea is supported by the

reproductive output of *Lactuca scariola*, another relatively late flowering species. The values found for reproductive output in this study are greater than those reported by Marks and Prince (1981) in Britain, but less than those reported by Stevens (1932) for North America.

2. Effects of seed predators

The potential reproductive outputs of 7 of the biennials in this study were found to be reduced by the actions of seed predators. Seed predation by goldfinches was estimated at 30% in *Cirsium vulgare*, *Lactuca scariola*, *Onopordum acanthium*, and *Tragopogon dubius*. Ridley (1930) stated that European goldfinches (*Carduelis carduelis* L.) also feed on seeds of *Dipsacus sylvestris*, but none of the capitula of this species in my study had any evidence of goldfinch activity. Werner (1975a) stated that an unidentified stem-boring lepidopteran larva occasionally infested stems of *Dipsacus sylvestris* and reduced seed production, but I found no evidence of any stem-borer activity. Flowering stalks of *Onopordum acanthium*, however, were often infested by the stem-boring larva of the lepidopteran *Papaipema nebris* (Guenee). Nearly 20% of the capitula of *Onopordum acanthium* had been destroyed by the activity of this insect. Fruits of *Verbascum thapsus* were infested by larvae of the curculionid weevil *Gymnaetron tetrum* Fab. Gross and Werner (1978) reported that larvae of this insect could destroy up to 50% of the seeds of *Verbascum thapsus*. In this investigation 35% of the *Verbascum thapsus* capsules sampled were infested with *Gymnaetron tetrum* larvae. Gross and Werner (1978) and I found that all seeds in an infested capsule were destroyed by the larvae. Although the larva of

Gymnaetron tetrum is reported to be host-specific for *Verbascum thapsus* (Gross and Werner 1978), I found that 2.0% of the capsules of *Verbascum blattaria* sampled in this study were infested with what were apparently larvae of *Gymnaetron tetrum*. Again, all seeds were destroyed in an infested capsule. Capitula of *Arctium minus* were infested by larvae of the burdock moth, *Metzneria lappella* Zeller. Hawthorn and Hayne (1978) reported that in southwestern Ontario infestations by the larvae of this species can result in the loss of 28-71% of the seed output of the infested plant. In southern Michigan Gross found that infestations of *M. lappella* resulted in 14-44% loss of seed output of the infested plant (Gross et al 1980). In the current study, seed losses to larvae of *M. lappella* represented approximately 74% of the seeds produced in the capitula of *Arctium minus* sampled.

With the possible exception of *Tragopogon pratensis*, each of the biennial species seems to produce sufficient seeds in the Marshall pit to ensure their continued regeneration (Table 3.2). Apparently only one of them, *Arctium minus*, has its population size greatly reduced by a seed predator. Historically however, *M. lappella* has proved an effective control for *Arctium minus*. Groh (1930) reported that *Arctium minus* was a serious agricultural weed in Canada before the introduction of burdock moth but after its introduction, *Arctium minus* became insignificant as an agricultural pest.

B. Mean weight per seed of the biennial species

Biennials are plants which occur in intermittent and semi-open sites such as woodland gaps, meadows, cedar glades, roadsides, dunes, abandoned

mine pits, abandoned quarries and abandoned fields where disturbance is not annual, but rather is unpredictable in time (Stevens 1932, Salisbury 1942, Holt 1972, Werner 1975b, Grubb 1976, Hart 1977, Werner 1977, Harper 1977, van der Meijden and van der Waals-Kooi 1979, Baskin and Baskin 1979a,b, Gross 1980b, van Leeuwen and van Breeman 1980, Heagy 1981, van Leeuwen 1981, Klemow and Raynal 1981, Gross and Werner 1982, Silvertown 1982, van Breeman and van Leeuwen 1983, van Breeman 1984, Klemow and Raynal 1985, Fenner 1985, de Jong and Klinkhammer 1986). Species which exploit such habitats are expected to have highly dispersable diaspores (Gadgil 1970). Since relatively small seeds are generally considered to be more readily dispersed than relatively large seeds (Salisbury 1942, Harper et al. 1970, Stebbins 1971, Stergios 1976, Wilbur 1977, Harper 1977, Silvertown 1982, Fenner 1985), biennials would be expected to produce relatively small seeds. Levin and Kerster (1974) report that the overall mean weight per seed of herbaceous plants worldwide is 7.0mg. The overall mean weight per seed of the 15 biennials in this study is 3.16mg, less than half the preceding mean. Only 3 of the biennial species included in this study, *Arctium minus* (on one sampling date), *Tragopogon pratensis*, and *Onopordum acanthium* had mean weights equal to or heavier than this mean (Table 3.3). When, however, a comparison was made of mean weight per seeds of herbaceous species of open, semi-closed, or closed vegetation, excluding the heavy-seeded perennials which dominate the understories of closed woodlands (Salisbury 1942, Harper et al. 1970, Baker 1972, Harper 1977, Silvertown 1982, Fenner 1985), seeds of biennials were found to be 3 to 4 times heavier than those of annuals or perennials (Thompson 1984). Thompson (1984) felt that the heavier seed weights of biennials conferred an advantage on their seedlings

relative to those of annual or perennial species in closed habitats and therefore allowed biennial species to exploit a wider variety of habitats than had been supposed previously.

Taking the antilog$_{10}$ of Thompson's (1984) transformed seed weight data, the mean weight per seed for herbaceous species (excluding those from closed woodlands) in Great Britain becomes 0.326mg for annuals, 1.27mg for biennials, and 0.469mg for perennials. The overall mean weight per seed for the 15 biennials in this study, 3.16mg, is nearly 2.5 times greater than that of the biennial species in Thompson's (1984) data set. Five of the biennials in this study, *Daucus carota*, *Lactuca scariola*, *Oenothera biennis*, *Verbascum blattaria*, and *Verbascum thapsus*, have mean weights per seed less than that reported by Thompson (1984) for biennials. Two of these, *Verbascum blattaria* and *Verbascum thapsus*, have mean weights per seed smaller than the mean weights reported for annuals (Table 3.3), and would in fact be classified as very small seeded species (Thompson 1984). Even though more than half of the biennial species in this study might be classified as relatively heavy-seeded species in this particular habitat (Thompson 1984), there is a wide range of mean seed sizes present among them (Table 3.3). The biennials in the Marshall pit as a group do not in all likelihood owe their continued success in that particular habitat to the possession of a larger seed than that produced by the annual and perennial species in the community.

Mean weights per seed for each of the 15 biennial species included in this study have been published previously. Seeds of *Alliaria petiolata* are reported to range in weight from 1.62mg in woodland edges in

southwestern Ontario to 2.84 ± 0.28mg in Britain (Cavers et al 1979, Grime et al 1981). *Arctium minus* was found to have a mean weight per seed which ranged from 6.0 ± 0.4mg in old fields in southern Michigan to 11.47mg in woodland margins in Britain (Gross et al 1980, Hawthorn and Hayne 1978, Reed and Stephenson 1973, Salisbury 1942, Stevens 1932, Grime et al 1981, Gross 1984). The range in weight of individual seeds of this species was reported to be from 4.78 to 13.14mg in old fields in southern Michigan (Gross 1984). The mean weight per seed of *Cirsium vulgare* was recorded as ranging from 2.0 to 4.0mg in dune systems in the Netherlands (van Leeuwen and van Breeman 1980, de Jong and Klinkhammer 1986) and was found to be 2.64mg in well-drained grasslands and meadows in Britain (Grime et al 1981). *Daucus carota* has a mean weight per seed which has been reported to range from 0.61mg to 1.5mg in old fields in southwestern Ontario and southern Michigan and in calcareous grasslands in Britain (Salisbury 1961, Dale and Harrison 1966, Dale 1974, Grime et al 1981, Lacey 1981, Gross and Werner 1982, Mittlebach and Gross 1984, Gross 1984). The range in weight of individual seeds of this species was found to be from 0.12mg to 2.22mg in old fields in Michigan (Gross 1984). The mean weight per seed of *Dipsacus sylvestris* has been reported to range from 1.1 ± 0.2mg in old fields in southern Michigan (Werner 1975a, Mittlebach and Gross 1984, Gross 1984) to 5.0mg in intermittently open habitats in Britain (Salisbury 1942) with a range in individual seed weights of from 0.69 to 2.56mg for individuals growing in old fields in southern Michigan (Gross 1984). *Echium vulgare* has a mean weight per seed which ranged from 2.7mg in a dune system in the Netherlands (van Leeuwen and van Breeman 1980, van Breeman 1984) to 2.76mg in sandy areas in Britain (Salisbury 1961, Grime et al. 1981). Mean seed weight of *Lactuca scariola*

was reported to be 0.45mg both in North Dakota (Stevens 1932) and in open habitats in Britain (Salisbury 1942). *Melilotus alba* has a mean weight per seed which was found to range from 2.2 to 2.7mg in Britain (Salisbury 1942) and to be 2.0mg in North Dakota (Stevens 1932). Cavers and Steel (1984) reported that the mean weight per seed of *Melilotus alba* near London, Ontario ranged from 1.2mg to 1.6mg. Salisbury (1961) recorded the mean weight per seed of *Melilotus officinalis* as 2.2mg in Britain. The mean weight per seed of *Oenothera biennis* was found to be 0.6mg in Britain (Salisbury 1961). In North America the mean weight of this species ranged from 0.19 ± 0.02mg for individuals growing on badger mounds in an Iowa prairie (Platt and Weis 1977) to 0.41 ± 0.08mg in old fields in southern Michigan (Stevens 1932, Gross and Werner 1982, Mittlebach and Gross 1984, Gross 1984). The range in weights of individual seeds of this species in old fields in southern Michigan was found to be from 0.080 to 0.477mg (Gross 1984). Cavers and Steel (1984) reported that the mean weight per seed of *Onopordum acanthium* growing near London, Ontario ranged from 10.2mg to 12.4mg. Stevens (1932) found that in North Dakota seeds produced by inner flowers of *Tragopogon dubius* weighed 4mg, whereas those produced by outer flowers weighed 6mg. The mean weight per seed of this species in old fields in southern Michigan was reported to range from 6.84 ± 1.16mg to 6.94 ± 0.23mg (Gross and Werner 1982, Mittlebach and Gross 1984, Gross 1984). The range in weights of individual seeds of *Tragopogon dubius* in the same habitats was from 1.97mg to 12.11mg (Gross 1984). Grime et al. (1981) recorded the mean weight per seed of *Tragopogon pratensis* in Britain as 4.69mg. Cavers and Steel (1984) found that the mean weight per seed of *Verbascum blattaria* growing near London, Ontario ranged from 0.10mg to 0.11mg. The mean weight of *Verbascum*

thapsus was reported to be 0.09mg in intermittently open habitats in Britain (Salisbury 1942, Grime et al. 1981) and in open habitats in North America from 0.05 ± 0.002mg to 0.09mg (Stevens 1932, Gross and Werner 1982, Mittlebach and Gross 1984, Gross 1984, Cavers and Steel 1984). In old fields in southern Michigan Gross (1984) found that the weight of individual seeds of this species ranged from 0.008mg to 0.015mg.

A comparison of the mean weights per seed of the biennial species in this study with those reported for these same species in the literature reveals that all but six of the biennials in this study have mean weights which conform to values previously recorded (Table 3.3). Of the species which have mean weights per seed which differ from recorded values, *Tragopogan pratensis* and *Lactuca scariola*, had a heavier mean weight per seed whereas *Cirsium vulgare*, *Echium vulgare*, *Melilotus officinalis* and *Tragopogan dubius* had lighter mean weight per seed than had been previously reported in the literature (Table 3.3). The reason why the mean weights per seed of these 6 species fell outside the range of published values is unclear. There are however, several possible explanations for these discrepancies. First of all, the small sample size that I used might have biased my calculations of the mean values. It is possible that other researchers included damaged plants or unripe seeds in their samples. Finally, in all likelihood my samples were more representative of the entire infructescence of an individual plant than were those of other researchers.

C. Variability of seed weight within a species

While the mean weight per seed of a species may be a relatively constant character (Salisbury 1942, Harper et al. 1970, Harper 1977, Silvertown 1982, Fenner 1985), studies have shown that within species mean weight per seed may vary considerably between populations in different habitats (Harper et al. 1970, Baker 1972, Werner and Platt 1976, Schimpf 1977, Primack and Antonovics 1981, Thompson 1981), within a single population (Harper et al. 1970, Wilbur 1977, Howell 1981, Verkaar and Schenkeveld 1984b, Waller 1982, Gross 1984), between individuals within a population (Wulff 1973, Waller 1982, Pitelka et al. 1983, Wulff 1986a) and within a single individual (Salisbury 1942, Black 1957, Koller and Roth 1964, Williams and Harper 1965, Cavers and Harper 1966, Evenari et al. 1966, McWilliams et al. 1968, Harper et al. 1970, Cavers and Maun 1971, Baker 1974, Cook 1975, Hendrix 1979, Gray 1979, Bentley et al. 1980, Schaal 1980, Gutterman 1980/1981, Willson and Price 1980, Waller 1982, Cideciyan and Malloch 1982, Ball and Quinn 1982, Weis 1982, Pitelka et al. 1983, Fuller et al. 1983, Zimmerman and Weis 1983, Cavers and Steel 1984, Stanton 1984, Venable and Levin 1985, Wulff 1986a). Within an individual plant, the variation in mean weight per seed can result from the position of fruits within the infructescence (Stevens 1957, Cavers and Harper 1966, Maun and Cavers 1971, Reed and Stephenson 1973, Harper et al. 1970, Gutterman 1980/81, Waller 1982, Koller and Roth 1964), the position of seeds within a fruit (Salisbury 1942, Harper et al. 1970, Hendrix 1979, Schaal 1980, Thompson 1981, Zimmerman and Weis 1983, Pitelka et al. 1983, Stanton 1984, Venable and Levin 1985, Wulff 1986a) or environmental conditions which were encountered by the maternal parent during flowering

and/or seed maturation. Examples of such environmental conditions are temperature (McWilliams et al. 1968, Gutterman 1980/1981), photoperiod (Cook 1975, Wulff 1986a), resource limitation (Willson and Price 1980), and loss of photosynthetic material due to grazing (Maun and Cavers 1971, Bentley et al. 1980).

1. Seed polymorphisms

For many plant species, particularly those which inhabit frequently disturbed or arid and semi-arid environments, the expression of the phenotype includes the production of two or more morphologically distinct types of seed (Harper et al. 1970, Harper 1977, van der Pijl 1982, Silvertown 1982, Silvertown 1984b, Fenner 1985). This condition is termed a somatic seed polymorphism (Harper et al. 1970, Harper 1977, van der Pijl 1982, Silvertown 1984b). In species which possess a somatic seed polymorphism, the different seed morphs normally have different ecological roles (Salisbury 1942, Harper et al. 1970, Harper 1977, Silvertown 1982, Silvertown 1984b, Venable and Levin 1985). Commonly the morphs have different colored seed coats; one morph is larger than the other; one morph is more dormant than the other; and/or one morph is more readily dispersed than the other (Salisbury 1942, Koller and Roth 1964, Williams and Harper 1965, Evenari et al. 1966, Harper et al. 1970, Baker 1974, Harper 1977, van der Pijl 1982, Silvertown 1982, Silvertown 1984b, Venable and Levin 1985, Fenner 1985). Such seed polymorphism provides an advantage for the species which possesses it because the seeds of that species are able to reach and exploit a much wider range of microsites both in space and in time than are seeds of a species which produces only

a single type of seed (Harper et al. 1970, Baker 1974, Harper 1977, Silvertown 1982, Silvertown 1984b).

2. Variation of seed weight within individual plants

Several recent studies of species having an extended fruiting period have shown that even though distinct seed morphs were not formed by these species, the mean weight of seeds produced by individual flowering plants varied throughout the fruiting period (Gray 1979, Bell and Quinn 1982, Fuller et al. 1983, Cavers and Steel 1984, Verkaar and Schenkeveld 1984b). Several suggestions have been put forth to explain why an individual plant might produce seeds of various weights over the course of its fruiting season. There could be a genetic basis for varying seed weight (Harper et al. 1970, Harper 1977, Silvertown 1982, Cavers and Steel 1984). Salisbury (1942) believed that the seeds formed initially by the plant might have first access to a limited food supply and hence be larger. The nutrient environment in which a plant is rooted could change during the course of the growing season and consequently the supply of nutrients available to the developing seed might not be constant (Cavers and Steel 1984). In late summer and early fall, the level of light intensity and the length of the photoperiod both decrease (Cavers and Steel 1984). Also plants may lose leaves to herbivores and individual leaves may senesce and be shed before seed maturation is complete (Cavers and Steel 1984). These factors could lead to rates of photosynthesis which are reduced as the growing season progresses and so lead to a decreased supply of nutrients being available to seeds formed later in the growing season (Cavers and Steel 1984). Finally, Pitelka et al.

(1983) felt that different sized seeds might be produced by a plant simply because there is a lack of selection for a uniform seed size beyond certain limits.

Of the 15 biennial species in this study which were sampled more than once, only *Verbascum blattaria* and *Verbascum thapsus* had a constant mean weight per seed for all three sampling dates; every other species had at least a small variation in mean weight per seed between sampling dates (Table 3.3). Cavers and Steel (1984), in their investigation of changes in mean weight per seed within individual plants of several species over time, found as a general pattern that mean weight per seed diminished significantly ($P<0.05$) over time, the largest seeds being produced first followed by progressively smaller seeds as the plant aged. Four species, *Melilotus alba*, *Onopordum acanthium*, *Verbascum blattaria* and *Verbascum thapsus* were common between their study and the current investigation. My study also had *Daucus carota* in common with that of Verkaar and Schekeveld (1984b) who investigated the seed output, including the change in seed weight over time, of some forbs in chalk grasslands. In both previously published studies the mean weight per seed of each of these five species declined significantly ($P<0.05$ for *Daucus carota*, *Onopordum acanthium* and *Verbascum blattaria*; $P<0.001$ for *Melilotus alba* and *Verbascum thapsus*) throughout the growing season (Cavers and Steel 1984, Verkaar and Schenkeveld 1984b). The results of my study are in direct contradiction to published findings. I found no significant difference ($P>0.05$) in mean weight per seed between sampling dates for *Daucus carota*, *Onopordum acanthium*, *Verbascum blattaria*, *Melilotus alba*, and *Verbascum thapsus* (Table 3.3). Two of the species in my

study, *Echium vulgare* and *Cirsium vulgare*, did have a significant ($P<0.05$) progressive decrease in mean weight per seed throughout the growing season, but 3 others, *Lactuca scariola*, *Oenothera biennis* and *Tragopogon dubius*, had a progressive significant increase ($P<0.001$) in mean weight per seed as the season progressed and *Arctium minus* had a significantly ($P<0.001$) greater mean weight per seed at the intermediate sampling date than at the early or late sampling dates (Table 3.3).

Several studies have found that in some species, including 4 of the biennials in the current study, the variation in mean weight per seed between individuals within a population was greater than that either between populations or within an individual (Wulff 1973, Primack and Antonovics 1981, Waller 1982, Pitelka et al. 1983, Cavers and Steel 1984, Wulff 1986a). In one study it was found that the overall mean weight per seed of *Onopordum acanthium* decreased by 18% as the growing season progressed, yet when the 9 plants which had been sampled were considered individually, change in mean weight per achene ranged from an 8% increase to a 43% decrease over the course of the growing season (Cavers and Steel 1984). Several reasons have been put forth to account for the intrapopulation variability in mean weight per seed which occurs between individuals of some species. Leafiness (Maun and Cavers 1971), plant shape (Salisbury 1942), and herbivory and parasitism (Maun and Cavers 1971, Hendrix 1979) have been shown to affect seed size in some species. There could be a genetic basis for a progressive change in seed weight (Cavers and Steel 1984). Differing microsite conditions as well as differing rates of maturation could result in different seed weights between plants (Cavers and Steel 1984). Variations

in the relative amounts of seed production from lateral, late-developing branches on the inflorescences of individual plants could also alter the pattern of seed weight change (Cavers and Steel 1984).

For each species in my study, seeds were repeatedly sampled from the same individuals, but bulk samples of seeds were made of all the seeds taken on a given sampling date, and the bulk sample was subsampled to get individuals for individual weighing. The failure to keep separate the seeds collected from each individual flowering stalk in all likelihood introduced sufficient variation into the calculated mean weight per seed for each species on each sampling date to obfuscate the actual differences in mean weight which occurred within individual plants as the growing season progressed. Consequently, great care must be taken in the interpretation of results from this investigation. There appears to be some evidence (Table 3.3), however, that at least 6 of the biennial species in the current study do have a change in mean weight per seed within individual plants over the course of the growing season.

If there is a difference in the mean weights of seeds produced by individual plants of some or all of the 15 biennials throughout the growing season, it could serve to function as a somatic seed polymorphism. There is evidence that at least in some species, there is a difference in germinability in seeds produced at different times during the fruiting period (Grant-Lipp and Ballard 1963, Gray 1979, Bell and Quinn 1982, Fuller et al. 1983). Other studies have shown that within a species, seed size affects dispersability (Stergios 1976), germinability and dormancy (Wulff 1973, Stergios 1976, Harper 1977, Schaal 1980, Gray 1979, Gutterman 1980/1981,

Cideciyan and Malloch 1982, Weis 1982, Pitelka et al. 1983, Gross 1984, Verkaar and Schenkeveld 1984a), seedling emergence, (Black 1956, Wulff 1986b), and seedling vigor and establishment (Black 1958, Harper et al. 1970, Fenner 1978, Harper 1977, Schaal 1980, Howell 1981, Cideciyan and Malloch 1982, Weis 1982, Pitelka et al. 1983, Gross 1984, Stanton 1984, Wulff 1986a, Wulff 1986b). Seed polymorphism would enable the seeds of an individual to reach and exploit a much wider variety of habitats, both in time and in space, than would be possible if that individual produced seeds with only one set of responses. Consequently, possession of a somatic seed polymorphism would be a considerable advantage to individuals of species such as the 15 biennials in this study which are confronted by the task of exploiting an extremely heterogeneous environment.

D. Seed dispersal

Gravel pits in southwestern Ontario tend to occur as islands or small archipelagos surrounded by agricultural fields. Each of the 15 biennial species included in this investigation is a ruderal, a common inhabitant of waste places, abandoned fields, roadsides, and riparian gravel banks in southwestern Ontario (2.1). A source of diaspores of each of these species was readily available for the colonization of the Marshall pit as soon as mining operations ceased. The population of each of the species in the study area is the result of at least one successful colonization event.

According to Harper (1977) the great majority of seeds of most species fall near the parent plant. While long distance dispersal of a diaspore is of unquestionable importance in the colonization of a new habitat, it is

apparently a relatively rare occurrence. The seed rain which falls within a gravel pit is composed primarily of diaspores which originate from the vegetation present in that pit, with the addition of a relatively small number of diaspores which originated from external sources, and with the loss of a relatively small proportion of the diaspores produced within the pit which are transported elsewhere (Harper 1977). Consequently, the effect of long distance dispersal of diaspores on the population dynamics of my 15 biennial species was considered to be negligible in the Marshall pit and was not included in this investigation.

The successful regeneration of each of the biennial species within the Marshall pit is dependent on their diaspores being dispersed to suitable microsites within the pit (Fenner 1985). The heterogeneous soil surface of the Marshall pit, together with the relatively open vegetation composed largely of annual and biennial species, present an annually shifting mosaic of microsites to diaspores of the biennial species. Differences among the biennial species in their ability to effectively place diaspores in available safe sites could strongly affect both the size and flux of populations of the species in the study area.

1. Comparison with published studies

There are records of the mode of dispersal of, and in some cases, the mean dispersal distance of diaspores of each of the 15 biennial species included in this study. Cavers et al. (1979) suggest that since 70 to 90% of dry seeds of *Alliaria petiolata* were picked up by a damp cloth, this species may be dispersed by external transport on animals. Burs of *Arctium minus*

cling to the coats of animals, but the burs also float and have been reported to blow for some distance over crusted snow during winter (Ridley 1930, Hawthorn and Hayne 1978, Gross et al. 1980, Heagy 1981). Achenes of *Cirsium vulgare* are readily transported by wind (Heagy 1981). In dune systems in the Netherlands van Leeuwen and van Breeman (1980) found that achenes of this species were blown more than 5m whereas de Jong and Klinkhammer (1986) reported that 55% of achenes of *Cirsium vulgare* fell within 1m of the parent plant and 10% were blown more than 32m. Mericarps of *Daucus carota* have the potential to be wind transported and can be blown for considerable distances over crusted snow during winter (Dale and Harrison 1966, Dale 1974, Lacey 1981, Heagy 1981, Lacey 1982). Lacey (1981) reported that the mean dispersal of diaspores of this species from isolated plants in the field in autumn was less than 2.5m and that no diaspores were dispersed more than 6.25m. In winter she found that 94.7% of diaspores of this species dropped onto crusted snow were blown more than 16m (Lacey 1981). Fruits of *Daucus carota* were also found to be transported in the coats of animals, particularly those with coarse fur (Dale 1974, Lacey 1981, Heagy 1981) and to be able to pass unharmed through the guts of horses (Salisbury 1964), roe deer, and cattle (Ridley 1930). Werner (1975a) noted that fruits of *Dipsacus sylvestris* are dropped passively from the parent plant, with 99.9% falling within 1.5m of the parent plant in old fields in southern Michigan. Fruits of this species also float in water for up to 16 days (Ridley 1930, Werner 1975a, Heagy 1981) and have been reported to be dispersed by European goldfinches (Ridley 1930). While plants of *Echium vulgare* can function as tumbleweeds (Ridley 1930), nutlets of this species are usually blown by the wind (Heagy 1981, Ridley 1930); a dispersal distance of about

5m was reported in a dune system in the Netherlands (van Leeuwen and van Breeman 1980). Nutlets of *Echium vulgare* have also been found to be transported in animal fur (Ridley 1930, Salisbury 1961, Heagy 1981). Achenes of *Lactuca scariola* are transported by the wind, by animals, and along roads and railroads by vehicles (Ridley 1930, Heagy 1981). Fruits of both *Melilotus alba* and *Melilotus officinalis* are readily dispersed with crop seeds, can be blown short distances by strong winds, float and so are dispersable by rainwash and stream flow, and will cling to both wet and dry clothing (Turkington et al. 1978). Ridley (1930) reports that diaspores of both species were able to pass unharmed through the gut of a horse. Turkington et al. (1978) found that two thirds of the fruits of *Melilotus alba* remain floating after 15 minutes of violent agitation. Seeds of *Oenothera biennis* are passively wind dispersed (Heagy 1981, Ridley 1930). Platt and Weis (1977) found that seeds of this species were blown a mean of 1.83 ± 0.04m on badger mounds in prairie vegetation. While seeds of *Oenothera biennis* have been reported to float poorly, they can be transported short distances by rainwash (Ridley 1930). Achenes of *Onopordum acanthium* have been reported to float for 2 days in water and to be transported by European goldfinches (Ridley 1930). Achenes of both *Tragopogon dubius* and *Tragopogon pratensis* are blown by the wind (Ridley 1930), potentially more than 250m from the parent plant (Gross and Werner 1982). Heagy (1981) also reports that achenes of *Tragopogon pratensis* may be transported by animals. Seeds of *Verbascum blattaria* are passively released from the parent plant (Heagy 1981). Seeds of *Verbascum thapsus* are reported to be wind dispersed, with movement of the flowering stalk either by a strong wind or by an animal being required to release the seeds (Gross and Werner 1978). Salisbury (1961) found

that most seeds of this species fall less than 12m from the parent plant, whereas Gross and Werner (1978) reported that in old fields in southern Michigan 93% of seeds of *Verbascum thapsus* fell less than 5m and 75% fell less than 1m from the parent plant. Heagy (1981) noted that seeds of this species could also be transported by animals.

I found that more than 97% of *Oenothera biennis* seeds remained floating in water that had been agitated for 15 minutes and that 100% of the seeds of this species floated for 24 hours (Table 3.5). Otherwise the results of this study are in general agreement with those published previously.

2. Wind dispersal

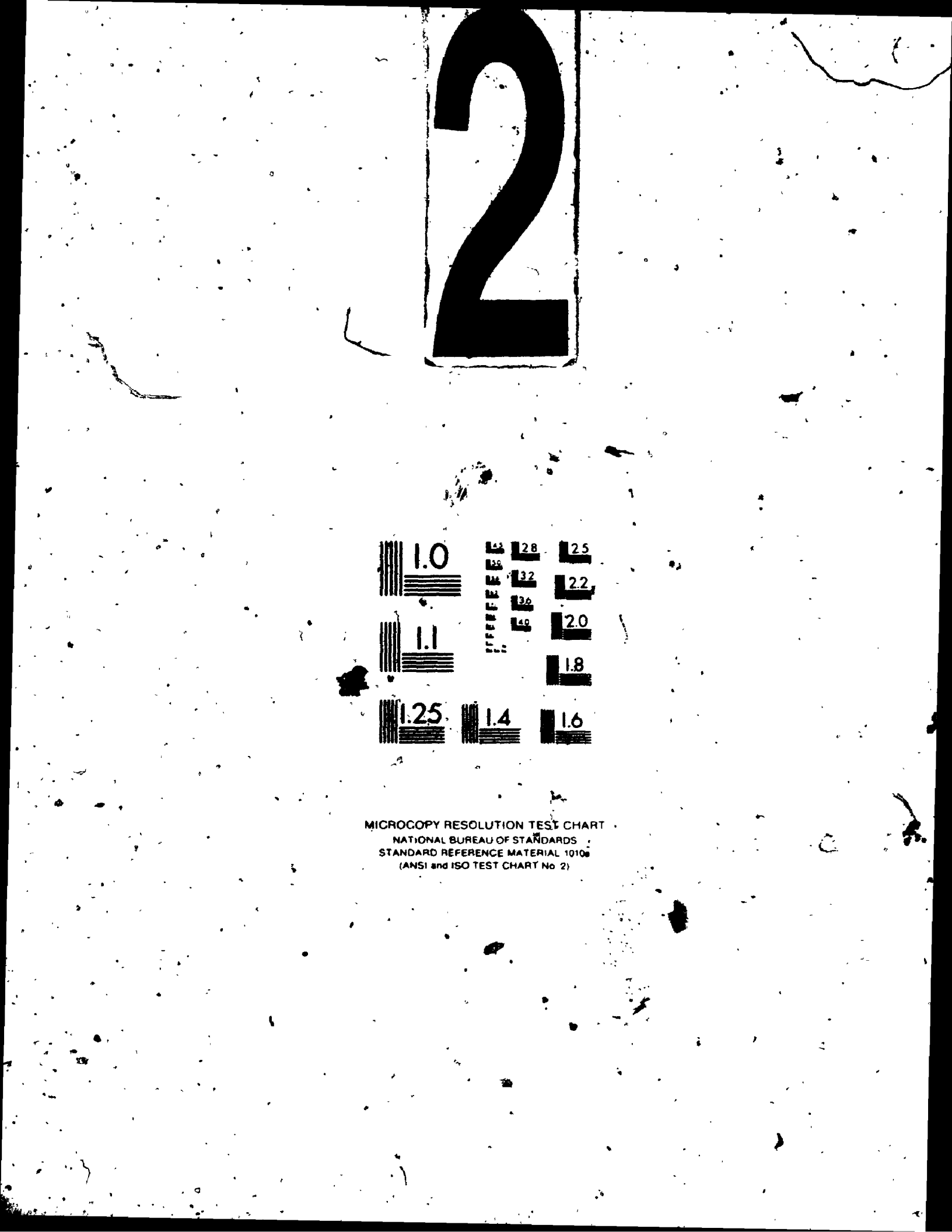
The biennial species in this study are all colonizers and as such have their diaspores dispersed primarily by either wind or external animal transport (Croxton 1928, Bramble and Ashley 1955, Schramm 1966, Viereck 1966, Byrnes and Miller 1973, Heagy 1981, van der Pijl 1982, Fenner 1985). The following is an examination of how diaspores of the biennial species are dispersed within the gravel pit by wind.

Any feature of a seed or fruit which reduces the speed with which it falls to the ground after its release will increase the probability of its being transported laterally by wind currents (Fenner 1985). Eight of the biennial species in this study have morphological features which appear to adapt them for wind dispersal. Seeds of the 2 lightest seeded species, *Verbascum blattaria* and *Verbascum thapsus*, are also very small and so each has a large surface area to volume ratio which produces wind resistance

and slows its descent (Harper 1977, Fenner 1985). More than 75% of the seeds of each of these species fell more than 1.0m from the drop point in this study (Table 3.4). Seeds of *Daucus carota* have rows of spines on them which increase the wind resistance of the falling diaspore and thereby increase the lateral distance covered during that fall (Lacey 1981). Seeds of *Cirsium vulgare*, *Lactuca scariola*, *Onopordum acanthium*, *Tragopogon dubius* and *Tragopogon pratensis* have pappi which are modified to increase the wind resistance of the diaspore during dispersal. Sheldon and Burrows (1973), in a laboratory study of dispersal in some species of the Compositae, found that while the size ratio of seed to pappus was important in determining the effectiveness of dispersal, the fine details of the geometry of the pappus which affected the aerodynamic properties of the diaspore had the greatest effect on the distance dispersed. In this study, the heaviest seeded species, *Onopordum acanthium*, had a relatively small open pappus and more than 60% of its diaspores fell more than 0.25 m from the drop point (Table 3.4), whereas two heavy seeded species *Tragopogon dubius* and *Tragopogon pratensis*, which had diaspores with a relatively large complex pappus, had more than 50% of their diaspores fall more than 1.0 m from the drop point. Two intermediate species, *Cirsium vulgare* and *Lactuca scariola*, which also had diaspores with a relatively large pappus, had 80% of their diaspores fall more than 1.0m from the drop point (Table 3.4). Care must be taken however, in the conclusions drawn from laboratory and isolated plant studies. Rabinowitz and Rapp (1980) found that differences in seed dispersal between species, which had been demonstrated under controlled conditions to be the result of differences in pappus geometry, were not apparent under field conditions.

In standing vegetation, surrounding plants hinder the dispersal of diaspores by reducing wind speed and by obstructing the flight paths of released diaspores (Sheldon and Burrows 1973). Consequently, most diaspores which are released within a stand of vegetation fall within or immediately adjacent to the stand (Ridley 1930, Poole and Cairns 1940 in Harper 1977, Sheldon and Burrows 1973, Stergios 1976). The obstructing effect of vegetation can be overcome if the height of an individual's flowering stalk is greater than the height of the surrounding vegetation (Fenner 1985). Further, Sheldon and Burrows (1973) demonstrated in still air in the laboratory that increased height of release of a diaspore results in increased lateral distance travelled. Individuals of each of the 15 biennial species included in this study may be present in some communities as isolated emergent plants with flowering stalks taller than all neighbors. However, the flowering stalks of each species are of approximately similar height (Table 3.1), and they formed a stand of roughly equal-sized stalks in the study area. Therefore it is expected that tall flowering stalks reduced wind speed and obstructed diaspore flight paths, thus causing most of the seeds produced by the biennial species in the study area to remain in or near that area.

For species in which a proportion of seeds are retained on the flowering stalk into the winter, wind can act as a dispersal agent by blowing diaspores over frozen ground or crusted snow (Ridley 1930). The importance of this phenomenon has been demonstrated in the dispersal of diaspores of both *Arctium minus* (Hawthorn and Hayne 1978) and *Daucus carota* (Dale and Harrison 1966, Lacey 1981). Potentially seeds of eight additional species



MICROCOPY RESOLUTION TEST CHART
NATIONAL BUREAU OF STANDARDS
STANDARD REFERENCE MATERIAL 1010a
(ANSI and ISO TEST CHART No. 2)

(*Dipsacus sylvestris*, *Echium vulgare*, *Melilotus alba*, *Melilotus officinalis*, *Oenothera biennis*, *Onopordum acanthium*, *Verbascum blattaria*, and *Verbascum thapsus*) could be dispersed within the study area during winter in the same manner.

In conjunction with the discussion of wind dispersal it should be noted that ten of the biennial species included in this study (*Alliaria petiolata*, *Arctium minus*, *Daucus carota*, *Dipsacus sylvestris*, *Echium vulgare*, *Melilotus alba*, *Melilotus officinalis*, *Oenothera biennis*, *Onopordum acanthium*, *Verbascum blattaria*, and *Verbascum thapsus*) have resilient flowering stalks. If the flowering stalk of one of these species is bent in one direction by a force such as a strong gust of wind or the passage of an animal, when the force is removed the stalk will vigorously spring back into its original position and in so doing will cast seeds some distance from the base of the plant (Ridley 1930, van der Pijl 1982). Additionally, when the flowering stalk of any of these species has senesced sufficiently that an applied force causes it to topple, any seeds which remain in it will be deposited at a distance away from the base of the plant (Ridley 1930).

3. Water dispersal

According to Ridley (1930), any diaspore which is light enough to be carried by the wind can also be transported by water. The distance the diaspore is carried is thought to depend on how long it remains impermeable to water (Ridley 1930). In this study it was found that the diaspores of all of the biennial species have the potential to be transported by calm

(*Dipsacus sylvestris*, *Echium vulgare*, *Melilotus alba*, *Melilotus officinalis*, *Oenothera biennis*, *Onopordum acanthium*, *Verbascum blattaria*, and *Verbascum thapsus*) could be dispersed within the study area during winter in the same manner.

In conjunction with the discussion of wind dispersal it should be noted that ten of the biennial species included in this study (*Alliaria petiolata*, *Arctium minus*, *Daucus carota*, *Dipsacus sylvestris*, *Echium vulgare*, *Melilotus alba*, *Melilotus officinalis*, *Oenothera biennis*, *Onopordum acanthium*, *Verbascum blattaria*, and *Verbascum thapsus*) have resilient flowering stalks. If the flowering stalk of one of these species is bent in one direction by a force such as a strong gust of wind or the passage of an animal, when the force is removed the stalk will vigorously spring back into its original position and in so doing will cast seeds some distance from the base of the plant (Ridley 1930, van der Pijl 1982). Additionally, when the flowering stalk of any of these species has senesced sufficiently that an applied force causes it to topple, any seeds which remain in it will be deposited at a distance away from the base of the plant (Ridley 1930).

3. Water dispersal

According to Ridley (1930), any diaspore which is light enough to be carried by the wind can also be transported by water. The distance the diaspore is carried is thought to depend on how long it remains impermeable to water (Ridley 1930). In this study it was found that the diaspores of all of the biennial species have the potential to be transported by calm

water, and that every species except for *Alliaria petiolata* and *Verbascum blattaria* has the potential for at least 10% of diaspores to be transported at least for short distances by flowing water (Table 3.5). While no ponds or streams are present within the study area, the implications of my findings are that diaspores of the biennial species which have been dispersed but not buried can be moved secondarily by water in a form which is present in quantity in the study area, namely snowmelt and rainwash. Even the nonbuoyant diaspores of *Alliaria petiolata* and *Verbascum blattaria* could be moved by saltation. Ridley (1930) and Salisbury (1961) both noted that secondary transport of dispersed seeds by rainwash might be the single most important means of local seed dispersal and that it results in further movement of the seed than is achieved through falling from the parent plant. In all likelihood movement of seeds by rainwash and snowmelt are important ways by which seeds of the biennial species are dispersed within the study area.

4. External transport by animals

Diaspores of only two of the biennial species included in this study, *Arctium minus* and *Daucus carota*, have obvious morphological adaptations for external animal transport. In a highly artificial experiment, I found that diaspores of each of these species could, to a greater or lesser extent, be transported at least short distances by adhering to the wet or dry fur of the intermediate sized mammals, ie: groundhogs (*Marmota monax* L.), raccoons (*Procyon lotor* L.), striped skunks (*Mephitis mephitis* Schreber), red foxes (*Vulpes fulva* Desmarest), and dogs (*Canis familiaris* L.), which were

observed to pass through the study area during the course of the investigation (Table 3.6). Seeds of 9 species, *Alliaria petiolata*, *Dipsacus sylvestris*, *Echium vulgare*, *Melilotus alba*, *Melilotus officinalis*, *Oenothera biennis*, *Onopordum acanthium*, *Verbascum thapsus*, and *Verbascum blattaria* adhered to the groundhog pelt in greater numbers when it was wet than when it was dry (Table 3.6). Although seeds of none of the species in my study are known to produce mucilage (Young and Evans 1973), diaspores of these 9 species apparently became stickier when they were wet. In all likelihood external transport by animals was most significant in their dispersal in the study area in conjunction with rain. Diaspores of both *Tragopogon* species however, had reduced ability to adhere to the wet pelt (Table 3.6). The diaspores of both these species contain a large intricate pappus which can become entangled in the fur of an animal. Many composite species have pappi which are hygroscopically active (Sheldon and Burrows 1973). Possibly the pappus of the diaspore of each *Tragopogon* species is fully extended when dry and thus is able to adhere to animal fur, whereas when wet it closes and loses this ability. No attempt was made to assess the potential of the diaspores of the biennial species to be transported by adhering to the feathers of birds. Presumably the hooks, barbs, and surface irregularities which allow their diaspores to be transported in the fur of animals would be as effective in clinging to the feathers of many species of birds (van der Pijl 1982).

Several studies have indicated that the fine details of the hooks and barbs present on a diaspore of a given species may determine which animal will act as the agent of dispersal for that species (Fenner 1985). In a study

observed to pass through the study area during the course of the investigation (Table 3.6). Seeds of 9 species, *Alliaria petiolata*, *Dipsacus sylvestris*, *Echium vulgare*, *Melilotus alba*, *Melilotus officinalis*, *Oenothera biennis*, *Onopordum acanthium*, *Verbascum thapsus*, and *Verbascum blattaria* adhered to the groundhog pelt in greater numbers when it was wet than when it was dry (Table 3.6). Although seeds of none of the species in my study are known to produce mucilage (Young and Evans 1973), diaspores of these 9 species apparently became stickier when they were wet. In all likelihood external transport by animals was most significant in their dispersal in the study area in conjunction with rain. Diaspores of both *Tragopogon* species however, had reduced ability to adhere to the wet pelt (Table 3.6). The diaspores of both these species contain a large intricate pappus which can become entangled in the fur of an animal. Many composite species have pappi which are hygroscopically active (Sheldon and Burrows 1973). Possibly the pappus of the diaspore of each *Tragopogon* species is fully extended when dry and thus is able to adhere to animal fur, whereas when wet it closes and loses this ability. No attempt was made to assess the potential of the diaspores of the biennial species to be transported by adhering to the feathers of birds. Presumably the hooks, barbs, and surface irregularities which allow their diaspores to be transported in the fur of animals would be as effective in clinging to the feathers of many species of birds (van der Pijl 1982).

Several studies have indicated that the fine details of the hooks and barbs present on a diaspore of a given species may determine which animal will act as the agent of dispersal for that species (Fenner 1985). In a study

similar to mine Lacey (1981) demonstrated that fruits of *Daucus carota* would not cling to the relatively fine fur of mice, but could only be transported on the coarser pelages of raccoons, striped skunks, or badgers (*Taxidea taxus* Schreber). In an artificial experiment conducted in the dry forest of Costa Rica in which the "animal" was a board covered with cloth, Bullock and Primack (1977) found that a dynamic equilibrium was established between the loading and unloading of diaspores. They found that diaspores of each species had a characteristic percentage of retention, mean dispersal distance, and height of attachment (Bullock and Primack 1977). In this and other studies it was found that even in plant species which are apparently highly adapted for external animal transport of their diaspores, only a small percentage of the diaspores produced are actually picked up by an animal (Fenner 1985). External transport of diaspores in the coats of animals is apparently at best an unreliable means of seed dispersal. External transport by animals is not believed to be an important means of seed dispersal for the biennial species in the Marshall pit because of the relatively small numbers of suitable animal agents which were oberved to inhabit or pass through the study during the course of this investigation.

Diaspores of relatively small-seeded species which have no obvious morphological adaptations for dispersal can be transported by animals in mud which adheres to their feet (Salisbury 1961, Fenner 1985). Darwin (1860) collected dried mud from the legs of a red-legged partridge (*Alectoris rufa* L.) and found that 82 seedlings of several species emerged from it. In my study, seeds of nine biennial species (*Alliaria petiolata*, *Daucus carota*, *Dipsacus sylvestris*, *Echium vulgare*, *Melilotus alba*, *Melilotus officinalis*,

Oenothera biennis, *Verbascum blattaria*, and *Verbascum thapsus*) are relatively small and are readily incorporated into the soil. It is probable that at least some seeds of these species are transported within the Marshall pit in dried mud adhering to the feet of individual birds and mammals.

Probably the most important means by which diaspores of each of the 15 biennial species are transported both within an existing gravel pit and into newly formed gravel pits however, is through carriage on automobiles, trucks, and heavy construction equipment (Salisbury 1961). Diaspores of any of the 15 biennial species could potentially be transported in crevices or on flat surfaces of such vehicles or encased in mud which adhered to their tires or chassis. Transport of diaspores in such a fashion is a form of directed dispersal which will allow ruderal species to rapidly colonize suitable man-disturbed habitats as soon as they become available.

5. Internal transport by animals

The potential for diaspores of the 15 biennial species included in this study to be dispersed internally by animals was not investigated since such dispersal has been reported to be rare among colonizing species (van der Pijl 1982, Harper 1977). Diaspores which are adapted for internal animal transport are normally encased in an attractive, nutritious fruit (van der Pijl 1982, Fenner 1985), and the diaspores of each of the biennial species in this study are dry. Ridley (1930) and Janzen (1984) both noted that seeds and seedlings of many herbaceous dicotyledons are found in the dung of livestock and old world herbivores. Small seeds which are consumed incidentally by herbivores as part of their fodder and which survive passage

through the gut are normally transported some distance from the location where they were ingested and are able to germinate in dung, a rich fertilizer, once they have been eliminated (Janzen 1984). Janzen (1984) has suggested that many herbaceous species which have no obvious morphological adaptation for dispersal may in fact be adapted for internal transport by a now largely extinct Pleistocene megafauna of grazers and browsers. Characteristics such as growth as isolated plants on fully insolated bare soil, production of a large number of small, hard, dormant seeds, retention of seeds within vegetative parts of the plant, and intermingling of fruits with relatively nutritious foliage on the flowering stalk are considered to be adaptations for internal transport by large herbivores (Janzen 1984). Nine of the biennial species included in this study (*Alliaria petiolata*, *Daucus carota*, *Echium vulgare*, *Melilotus alba*, *Melilotus officinalis*, *Oenothera biennis*, *Onopordum acanthium*, *Verbascum blattaria*, and *Verbascum thapsus*) have this particular set of characteristics and may have evolved to be dispersed through the gut of large herbivores. According to Janzen (1984) this suite of characteristics should also be advantageous for the colonization of fields, pastures, roadsides, and other man-disturbed sites; hence the proliferation of such species as weeds today.

In summary, the 15 biennial species included in this study have the potential to employ a variety of mechanisms to disperse their diaspores. Often several of these mechanisms may be employed by a single species. Apparently none of these biennial species is limited in its distribution within the study area because of a failure to place its diaspores in microsites which are suitable for seed germination and seedling establishment.

Chapter 4

Seed Bank Dynamics

4.1 Introduction

The diaspores which fall within a given community are collectively termed the "seed rain" (Harper 1977). A seed rain is composed both of diaspores produced by individuals present within a given community and of those produced in other communities that are dispersed into that community (Harper 1977). For populations of species which do not have the capacity for vegetative propagation (*sensu* Silvertown 1982), such as the 15 biennials included in this study, the seed rain is the source of new individuals for both expansion and for the replacement of individuals which die within a population (Harper 1977).

Once dispersed, a seed, if it escapes predators, is confronted by an extremely heterogeneous environment (Harper 1977, Fenner 1985). Werner (1979) has suggested that, from the perspective of a plant, the environment may be perceived as a matrix where seeds do not germinate or seedlings do not establish, interspersed with locations where seeds do germinate and seedlings do establish. Harper (1977) used the term 'safe site' to describe locations where the stimuli required for breaking dormancy, the conditions required for germination, and the resources which are consumed during germination are provided, while predators, pre-emergence pathogens, competitors and toxic soil constituents are absent. As defined, a safe site is highly species specific (Harper 1977). The presence, abundance, and

distribution of individuals of a species within a given community may well reflect the numbers and distribution of its safe sites within that community (Harper 1977).

In theory, a seed could be expected to germinate as quickly as possible after its dispersal from the parent plant. An individual which minimizes the time it spends as a relatively nutritious seed before it becomes a less nutritious vegetative body reduces the risk of being eaten (Janzen 1971, Angevine and Chabot 1979). Further, within a given species, seeds which germinate early often have been shown to produce seedlings which are at a considerable competitive advantage over late-emerging seedlings (Ross and Harper 1972, Baskin and Baskin 1972, Arthur et al. 1973, Hawthorn and Cavers 1976, Symonides 1977, Weaver and Cavers 1979, Cook 1980, Gross 1980, Howell 1981).

In nature many, if not most, diaspores of species which are dispersed randomly by agents such as gravity, wind, water, or external animal carriage are deposited in microsites which are not safe at the time of their deposition. A microsite is only safe in retrospect (Fenner 1985). Normally the seed is the stage of the plant life cycle which is most resistant to competition and able to tolerate adverse environmental conditions (Harper 1977, Cavers 1983, Fenner 1985). However, the seedling has been shown to be extremely vulnerable to adverse environmental conditions and to competition both from other seedlings and from established vegetation (Darwin 1860, Harper 1967, Naylor 1972, Sarukhan and Harper 1973, Sharitz and McCormick 1973, Harper and White 1974, Kawano and Nagai 1975, Werner 1975a, Werner 1975b, Hawthorn and Cavers 1976, Mack 1976, Symonides 1977, King 1977b, Werner 1977,

Turkington et al. 1978, Cavers et al. 1979, Baskin and Baskin 1979a, Baskin and Baskin 1979b, van der Meijden and van der Waals-Kooi 1979, Cook 1979, Gross 1980b, Schaal 1980, Klemow and Raynal 1981, Silvertown and Dickie 1981, Marks and Prince 1981, Gross and Werner 1982, Verkaar and Schenkeveld 1984a, Young 1984, de Jong and Klinkhammer 1986). When a seed germinates, the individual has literally 'bet its life' that environmental conditions will remain favorable for the subsequent establishment of the seedling (Angevine and Chabot 1979). It is imperative that a dispersed seed be able to accurately 'interpret' its immediate environment and then respond appropriately to the prevailing conditions. For most species, a seed that has been deposited in a microsite which it interprets as having a low probability of providing conditions which will be appropriate for subsequent establishment of a seedling, will delay germination by becoming dormant (Harper 1977, Silvertown 1982, Fenner 1985). A dormant seed maintains the possibility that in time it might encounter environmental conditions which will be favorable for subsequent seedling establishment and be stimulated to germinate (Fenner 1985). Both Harper (1977) and Fenner (1985) have suggested that after dispersal, seeds of most species undergo a period of dormancy which might extend from a few days to several years depending on the species and the prevailing environmental conditions.

Harper (1977) has identified 3 broad classes of seed dormancy. Innately dormant seeds are incapable of germination when freshly dispersed, even when conditions suitable for seedling establishment are available (Harper 1977). This type of dormancy may result from an immature embryo, a seed coat which is impermeable to oxygen or water; the presence in either the

seed coat or the embryo of inhibitory chemical compounds, or a requirement for specific environmental conditions such as chilling, fluctuating temperatures, or particular photoperiods (Harper 1977, Fenner 1985). Innate dormancy serves either to stagger germination or to delay it to the most favorable season (Harper 1977, Fenner 1985). Enforced dormancy results from the seed being deprived of its requirements for germination, for example oxygen, water, light, or suitable temperatures (Harper 1977, Fenner 1985). This form of dormancy involves no particular physiological mechanism, and a seed will be capable of germination as soon as the limiting requirement is provided (Harper 1977, Fenner 1985). Enforced dormancy serves to prevent a seed from germinating into circumstances which will prove unfavorable for seedling establishment. If seeds of a species which possesses no innate dormancy are dispersed into a location where they fail to find suitable conditions for germination, dormancy may be induced within them (Harper 1977, Fenner 1985). This form of dormancy is physiological in nature and requires specific environmental conditions such as chilling, fluctuating temperatures, or particular photoperiods to break (Harper 1977, Fenner 1985). Induced dormancy allows a seed to exploit favorable conditions immediately, but also provides it with the option to delay germination until the most favorable season. Seeds of a given species may employ only one, or they may employ some combination of these mechanisms in their dormancy behavior (Harper 1977, Silvertown 1982, Fenner 1985).

A dormant seed normally becomes incorporated into the soil seed bank. Roberts (1981) defines the seed bank as the reserve of viable seeds which are present in the soil or on its surface. Thompson and Grime (1979), in

a survey of germinable seeds contained in soil samples collected from 10 plant communities in Britain, organized the seed banks formed by the species they encountered into four categories. Some species had transient seed banks which were present only in summer, others had transient seed banks which were present only in winter (Thompson and Grime 1979). Most seeds of some species germinated immediately after dispersal, but a small proportion became incorporated into a seed bank which persisted throughout the year (Thompson and Grime 1979). Only a few seeds of other species were able to germinate immediately after dispersal and most became incorporated into a relatively large seed bank which persisted throughout the year (Thompson and Grime 1979).

The ability to form a persistent seed bank can fulfill two roles in the population dynamics of a plant species. Colonizing species can, through this mechanism, adopt a strategy of dispersing their seeds through time so that rather than seeking out disturbances, they are able to have their seeds persist quiescently *in situ* in the soil in a habitat which has become unfavorable until another disturbance allows them to germinate and recolonize the habitat (Harper 1977, Silvertown 1982, Fenner 1985). Dormant seeds contained in a persistent seed bank also have genetic implications for a plant population (Harper 1977). Normally the seeds in a persistent seed bank have been contributed by several generations of plants (Harper 1977). These seeds provide a 'memory' for the population of the past environmental conditions which were encountered by previous generations (Harper 1977).. When a disturbance allows the germination of such a mixture of seeds, the resulting plants are progeny of parents which lived at

different times (Harper 1977). Silvertown (1982) has suggested that genetic exchange among individuals within such a population could result in the buffering of genetic change within that population.

Once incorporated into a persistent seed bank, seeds of many species have a potential longevity which has been shown anecdotally to extend for several decades (Harper 1977, Silvertown 1982, Fenner 1985). Roberts and Feast (1973) and Roberts (1981) have found that, under natural conditions, however, the numbers of viable seeds contained in seed banks formed by arable weeds decline exponentially over time. In cultivated ground the rate of loss of individuals from these seed banks was increased because seeds brought to the surface germinated (Roberts and Feast 1973, Roberts 1981). In undisturbed ground the rate of loss of individuals was decreased, but the majority were lost to predators and pathogens rather than through germination and successful seedling emergence (Roberts and Feast 1973, Roberts 1981).

A seed which has been incorporated into a persistent seed bank runs a constant risk of mortality (Roberts and Feast 1973, Roberts 1981, Harper 1977, Fenner 1985). To reduce this risk it should germinate as soon as surface environmental conditions are favorable for subsequent seedling establishment. Plant species employ a variety of intricate and subtle mechanisms whereby their dormant seeds are able to 'recognize and interpret' a range of diverse environmental cues and as a result either remain dormant or break dormancy and become stimulated to germinate (Harper 1977, Angevine and Chabot 1979, Silvertown 1982, Fenner 1985).

In seasonal climates, a season in which environmental conditions are favorable for seedling establishment is often followed by another in which they are not. It is advantageous for a dormant seed to be able to 'predict' in a broad sense which season will follow the current one. Both fluctuating temperatures (Harper 1977, Grime 1979, Angevine and Chabot 1979, Silvertown 1982, Fenner 1985) and the length of the photoperiod (Isikawa 1954) are employed by some north temperate species to indicate whether the current season will be followed by the lethal conditions of winter or the favorable conditions of spring. Increases in nitrate ions have been shown to promote seed germination in many species (Steinbauer and Grigsby 1957). Since the concentration of this ion in soil fluctuates seasonally in response to the changing activity of the soil microflora, an ability to respond to changes in the concentration of nitrate ions could act to promote seed germination during the most favorable season (Fenner 1985). In arid habitats rainfall is often seasonal or unpredictable. Seeds of many species which exploit such habitats contain chemical germination inhibitors in either the embryo or the seed coat (Harper 1977, Angevine and Chabot 1979, Fenner 1985). A critical minimum amount of water is required to leach out such inhibitors before a seed can germinate (Harper 1977, Angevine and Chabot 1979, Fenner 1985). In this fashion the seed is prevented from germination until there is a high probability that sufficient water will be present to supply the emerging seedling until it can become established (Harper 1977, Angevine and Chabot 1979, Fenner 1985).

During the time it spends in the seed bank, a seed may become buried so deeply that its stored food reserves are insufficient to support an

emerging seedling until it reaches the soil surface. Seeds of many species possess depth-sensing mechanisms which prevent their germination until they are located at a distance which their emerging seedlings can traverse. Many, if not most, very small-seeded species have a light requirement for germination (Harper 1977, Silvertown 1982, Fenner 1985). Wesson and Wareing (1969a) found that in many species freshly ripened seeds had no dormancy, but that if these seeds were buried in soil, they rapidly developed a light requirement for germination. A covering of soil also acts as an insulator and buffers a buried seed from extreme diurnal temperature fluctuations (Harper 1977, Fenner 1985). Such temperature fluctuations are greatly reduced with increasing soil depth (Harper 1977, Fenner 1985). A buried seed therefore can use the magnitude of temperature fluctuations to 'judge' its depth of burial. The composition of the soil atmosphere also changes with increasing soil depth, becoming relatively richer in carbon dioxide and relatively poorer in oxygen (Harper 1977, Fenner 1985). Popay and Roberts (1970) found that for at least some species low levels of oxygen and high levels of carbon dioxide inhibited germination. A seed in a seed bank can potentially use the composition of the soil atmosphere to gauge whether or not it lies within a depth for successful emergence.

Regeneration of plants from seed within most communities is dependent on the formation of gaps in the foliar canopy (Cavers and Harper 1967a, Holt 1972, Platt 1975, Grubb 1976, Harper 1977, Grubb 1977, Fenner 1978, Cook 1979, Thompson and Grime 1979, Silvertown 1982, Gross and Werner 1982, Gross and Werner 1983, Hartgerinck and Bazzaz 1984, Reinartz 1984b, Fenner 1985). Emerging seedlings normally are unable to capture sufficient resources

to compete with established vegetation, and the prevention of germination under such circumstances will preserve a seed for potentially more favorable conditions in the future (Harper 1977, Fenner 1985). The creation of a canopy gap results in conditions in which competition is either reduced or absent (Harper 1977, Fenner 1985). Gaps of various sizes are constantly formed in a plant community through natural disasters, the activities of animals, or the death of established individuals (Fenner 1985). Environmental conditions are radically different within a gap from those in the surrounding vegetation and so levels of light, water, and temperature can be used by dormant seeds to detect the presence of open ground (Fenner 1985). A cover of vegetation acts as an insulator which reduces the magnitude of diurnal temperature fluctuations (Harper 1977, Fenner 1985). A buried seed which experiences widely fluctuating diurnal temperatures is likely to be located in a gap (Thompson and Grime 1983, Fenner 1985). Sensitivity to varying light quality is another mechanism used by some species to detect gaps (Harper 1977, Fenner 1985). Light which is transmitted through a leaf canopy is relatively poor in wave lengths from the red portion of the spectrum and its ratio of red to far-red radiation is greatly reduced (Harper 1977, Fenner 1985). A seed in the seed bank which receives incident radiation with a high ratio of red to far-red wavelengths is not situated beneath a foliar canopy (Harper 1977, Fenner 1985). There is normally relatively little diurnal variation in the levels of soil and atmospheric moisture present within standing vegetation (Fenner 1985). In contrast, on open ground evaporation is greatest during the day and least at night and much larger diurnal fluctuations are experienced (Fenner 1985). Thus, if a buried seed is exposed to diurnal cycles of favorable and unfavorable hydration, it is,

in all likelihood, not beneath a foliar canopy.

Biennials have been characterized as species having poor dispersal in space but wide dispersal in time (Harper 1977). They are held to be opportunists, colonizers of bare ground and unpredictable habitats which produce a large single crop of highly dormant seeds (Harper 1977). It is believed that, rather than seek out disturbances, biennials have adopted a strategy of building up a long lived persistent seed bank and remaining *in situ* until another disturbance provides their seeds with suitable conditions for emergence and establishment (Harper 1977).

The dynamics of the seed bank are of vital importance to species which employ such a life history strategy. In this chapter the behavior of the seeds of the 15 biennial species with regard to germination and dormancy was investigated in a controlled environment; the rain of diaspores of the biennial species which fell within the study area was surveyed, and the potential for each of the biennial species to build up persistent soil seed banks (*sensu* Thompson and Grime 1979) was assessed. Comparisons were made among the biennial species to attempt to identify variation in these life history characteristics. Where variations in life history characteristics were found, an attempt was made to determine whether or not these could potentially contribute to the coexistence of the 15 biennial species within the study area.

4.2 Materials and Methods

A. Predispersal seed viability

A study was carried out to determine what percentages of the 1981 seed crops of the 15 species were capable of germination, were dormant, or were non-viable. In this section of this chapter the word 'seed' is used in a very specific sense to refer to the product of a ripened ovule. As seeds became ripe in the field, they were collected and processed. For each species bulk samples of fruits were collected in the Marshall, Hill, and West Missouri gravel pits. Once collected, fruits were kept dry at ambient temperatures until processing could be completed. The processing of seeds differed according to the nature of the fruits of the individual species. For *Daucus carota*, *Dipsacus sylvestris*, *Echium vulgare*, and *Onopordum acanthium*, infructescences were pulled apart by hand to separate seeds, whereas for *Alliaria petiolata*, *Arctium minus*, *Melilotus alba*, *Melilotus officinalis*, *Oenothera biennis*, *Verbascum blattaria*, and *Verbascum thapsus* individual fruits were mechanically ruptured to release seeds. For these 11 species, the resultant material was passed through a nest of soil sieves with graded mesh sizes. Seeds were then separated from the residue of the fruits by means of a commercial seed blower. Fruits of *Cirsium vulgare*, *Lactuca scariola*, *Tragopogon dubius*, and *Tragopogon pratensis* were collected and the pappus removed by hand. The cleaned seeds were used to create a bulk sample for each of the 15 species.

For each species ten lots of seeds were removed from the bulk sample. Because their seeds were large, each lot of seeds from both species of

Tragopogon consisted of 50 seeds; each lot from the remaining 13 species consisted of 100 seeds. Each lot from every species was placed on two layers of filter paper. The upper layer was Green's # 400 and the lower layer was Whatman's # 2. The seeds were then moistened with 10ml of distilled water. Glass petri plates (9.5cm diameter) containing seeds of *Tragopogon dubius* and *Tragopogon pratensis* were placed in an incubator under a 16hr photoperiod and a 12hr/12hr, 30/15C alternating temperature regime. The higher temperature began 2.5hr after the beginning of the light period and ended 1.5hr before the end of the light period. Petri plates containing seeds of the remaining species were placed in an incubator under a 14hr photoperiod and a 12hr/12hr, 25/15C alternating temperature regime. The higher temperature began 1hr after the beginning of the light period and ended 1hr before the end of the light period. In each case the germination regime was designed to simulate conditions in the field when seeds became ripe. Germination was monitored every three days during the period of rapid germination and weekly thereafter. Protrusion of the radicle beyond the seed coat was the criterion for germination. Germinated seeds were removed from their respective petri plates once their germination had been recorded. Throughout the period of germination, petri plates were re-moistened with distilled water as needed to prevent the desiccation of seeds.

Once a given species had gone one week with no germination, its petri plates were removed from the incubator, sealed in metal canisters and stored for 6 months at 6.5C. Seeds of *Alliaria petiolata* had not germinated, so they were covered by a thin layer of potting soil in their petri plates before being sealed into canisters (following a suggestion of P.B. Cavers, personal

communication). No treatment was applied to seeds of any other species during this stratification treatment.

After stratification was concluded, all petri plates were removed from their canisters and the number of seeds which had either germinated or rotted was recorded. Then the petri plates were placed in an incubator under a 14hr photoperiod and a 12hr/12hr, 20/10C alternating temperature regime where the higher temperature began 1hr after the beginning of the light period and ended 1hr before the end of the light period. Germination was monitored as before.

Once a given species had gone 1 week with no germination, the petri plates containing seeds of that species were removed from the incubator. The remaining sound seeds were tested with tetrazolium chloride to determine their viability (Machlis and Torrey 1956). For each petri plate the embryos were dissected from all sound seeds and placed in a solution of 2,3 5-tetrazolium chloride in a small vial. The embryos of *Verbascum thapsus, Verbascum blattaria, and Oenothera biennis* were placed in a 0.01% solution of tetrazolium chloride because of their small size. The embryos of the remaining 12 species were placed in a 1.0% solution of tetrazolium chloride. All vials of embryos were stored for at least 24hr in a dark, heated cabinet at 40C. Then the vials were removed from the cabinet and the number of embryos which had turned red was recorded. All such embryos were assumed to represent viable seeds since the uptake of red stain indicated the presence of respiratory activity in the embryo (Machlis and Torrey 1956).

For each species the cumulative percent germination was separated into two segments: pre-stratification and post-stratification. From the results of the tetrazolium tests, the number of seeds of each species which were viable yet failed to germinate was determined also. The pre-stratification percent germination, post-stratification percent germination, and the percentage of viable ungerminated seeds were added to determine the total number of viable seeds for each species. Before analysis of these percentages, they were angular transformed to insure that the variance and mean were independent (Sokal and Rohlf 1981).

Values for each category (pre-stratification germination, post-stratification germination, viable ungerminated seeds, and total seed viability) were compared separately across all species. A one way analysis of variance was performed using the General Linear Model of the Statistical Analysis System (SAS Institute 1982). In any case where the F test was significant, Tukey multiple pairwise comparisons of the means were performed using the General Linear Model of the Statistical Analysis System (SAS Institute 1982).

B. Seed rain

The grid of horizontal and vertical transects established throughout the study area (2.2 A) was used as a framework for systematic sampling of the seed rain. This sampling was accomplished through the deployment of 129 seed traps of the design described by Werner (1975c). Each trap consisted of the lid of a 9.0cm plastic petri plate glued onto a 6cm x 6cm square of masonite and them mounted onto a 14.0cm wooden dowel sharpened

at its base. Four drainage holes were punched through the petri plate lid with heated nails to prevent water from standing in the trap. The traps were armed by placing a piece of Whatman's # 2 filter paper inside the petri plate lid and spraying it with "Tangletrap", a sticky substance which adheres to anything which touches it. One trap was placed at each intersection of a horizontal and vertical transect throughout the study area. Each trap was positioned such that the petri plate lid rested at soil surface level. Filter papers were replaced in the traps at weekly intervals from the initiation of the survey on June 7, 1981 until its termination on October 20, 1981. This termination date was chosen when regular frosts began to reduce the effectiveness of the "Tangletrap". The filter papers collected from the seed traps were brought back to the laboratory where the seeds adhering to them were identified. Once identified, the seeds were tested for soundness. All seeds which were firm and resistant to gentle pressure were assumed to be viable. Roberts and Ricketts (1979) found this to be a reliable method of determining viability in large lots of seeds.

For each species, the total number of sound seeds captured during the study period was determined and the mean number of seeds/m^2 was calculated. The expected composition of the seed rain was also estimated. From the 1982 vegetation survey (2.2 F.) the number of square meters in the primary study area which contained at least one flowering individual of each biennial species was known. The mean reproductive output for each biennial species was also known (Table 3.2). Through multiplying the mean reproductive output of each species by the number of square meters in the study area which contained at least one flowering individual of tha species, an estimate

of the gross number of seeds produced by each species within the primary study area was calculated. This method was believed to be too conservative for *Daucus carota*, the most abundant species in the standing vegetation (Table 2.2), so its contribution to the seed rain was estimated by assuming three flowering individuals for every square meter where it occurred. The gross number of seeds produced per species was reduced to the number of sound seeds produced per species by multiplying the gross reproductive output by the percent of viable seeds for that species. The number of sound seeds produced by each species per meter square was then calculated. This expected seed production per meter square was compared to the observed seed production per meter square by means of a chi-square test for goodness of fit. According to Sokal and Rohlf (1981), before a chi-square test for goodness of fit can be considered to be legimate, the smallest expected value should be 5 or greater. Since no seed production was expected from *Alliaria petiolata*, *Dipsacus sylvestris*, and *Tragopogon pratensis* (Table 3.2), these three species were omitted from the calculation.

C. Seed bank

The one hundred and six 5m x 5m squares formed by the grid of horizontal and vertical transects established over the study area (2.2 A.) were used as a framework for systematic sampling of the seed bank. Six sets of soil cores were collected, approximately one collection per month from late June through late October 1980. One set was collected in late April 1981. During a given sampling session a total of 53 soil cores were taken, with one core being taken from the same position within every second

one of the 106 5m x 5m squares in the sampling grid (Figure 4.1). In this fashion a uniform representation of the study area was obtained within each set of soil cores. In early June 1980 a set of soil cores was sent to the Soil Testing Laboratory at the University of Guelph for analysis of pH, soil texture and total phosphorus, potassium and magnesium (2.2 D.).

Each soil core was collected using a 10.0cm long by 9.5cm (inside diameter) stainless steel pipe which had been sharpened at the base. Each sample taken to a depth of 7.0cm and with a volume of approximately 500cm^3 was removed and placed in a plastic bag.

Once collected, the soil cores were taken to a greenhouse where they were placed in shallow clay dishes (22.5cm diameter x 4.2cm depth). These dishes were then placed on potting benches which had been covered in 2.5cm of peat moss. Both the soil in the dishes and the peat moss bed were kept moist by frequent watering. A given set of soil cores remained undisturbed for 8 weeks after which time the soil in each dish was stirred. The set of soil cores remained undisturbed for another 8 weeks, then they were rebagged individually and placed in a cold room at 7C for a period of time which related to the date on which they were collected. Those soil cores collected in late June remained at 7C for 16 weeks, whereas those collected in late July, late August, late September, and early November remained for 12, 8, 4, and 0 weeks respectively. On February 11, 1981, all sets of soil cores were placed in an unheated barn for 7 weeks. The set of soil cores collected in late April 1981 remained at 7.0C for 24 weeks and subsequently spent 8 weeks in an unheated barn. After being removed from the barn, all 6 sets of soil cores were placed again in shallow clay dishes on a bed

Figure 4.1. Diagram of one 5m x 5m block in the sampling grid showing the temporal sequence of collections of soil cores.

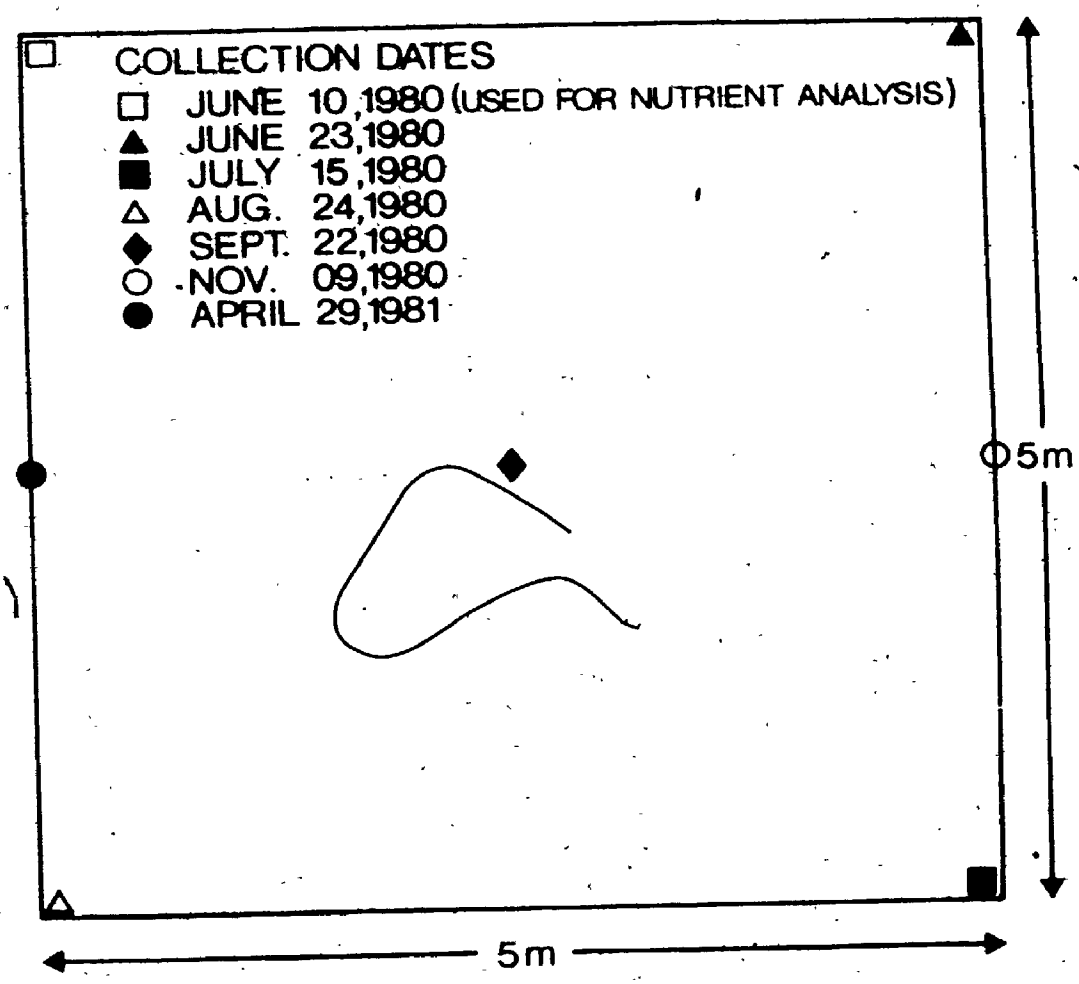


DIAGRAM OF ONE 5m x 5m BLOCK IN THE SAMPLING GRID SHOWING THE TEMPORAL SEQUENCE OF COLLECTIONS OF SOIL CORES

of peat moss where they remained undisturbed for 8 weeks before being stirred; then they remained undisturbed for 8 weeks more before the termination of the study.

During the periods that the soil cores were in the greenhouse, seedling emergence of biennial species of interest was recorded. Once a seedling had emerged and been identified, it was removed from the dish. This technique has been used to assess the composition of seed banks, but it fails to recover the viable seeds in the soil which do not germinate (Thompson and Grime 1979).

To gain an idea of the number of dormant seeds in the soil, a census using a modification of Malone's (1967) technique was performed on the set of soil cores from July, the month believed to have the smallest seed bank, and November, the month believed to have the largest seed bank. First, the individual soil cores were placed in 8l buckets and a solution of 1.0 l of water, 10.0g of magnesium sulphate and 50.0g of sodium hexametaphosphate was added to each. The soil was agitated well and the mixture allowed to stand for at least 1hr. During this time any organic matter present in the soil core should rise to the surface of the aqueous solution (Malone 1967). After the mixture had settled, the supernatant liquid was decanted into a nest of Canadian Standard sieves sizes 8 and 65 and washed with a gentle stream of water. The material held by the number 8 sieve was sorted by hand immediately for seeds of biennials whereas that held by the number 65 sieve was spread on a Whatman's # 1 filter paper and placed in a shallow clay dish on a potting bench in the greenhouse to air dry. Once dried, the sample was hand-sorted for seeds of biennials. The second step of the

extraction used the solid residue from the first step. A solution of 1.0 l of water, 10.0g of sodium bicarbonate and 50.0g of sodium hexametaphosphate was added to the residue. The mixture was agitated well and allowed to rest for at least 1hr. During this time clay colloids were dispersed and seeds were made easier to separate from the soil matrix (Malone 1967). After the mixture had settled, it was poured through a nest of Canadian Standard sieves sizes 3, 8, 18, and 65, and washed with a gentle stream of water. The materials held by the numbers 3, 8, and 18 sieves were sorted by hand immediately for biennial seeds. The material held by the number 65 sieve was spread on Whatman's # 1 filter paper and placed in a shallow clay dish on a potting bench in the greenhouse to air dry. The dried sample was then hand-sorted for seeds of biennials. Once sorted, all seeds were identified and tested for soundness. All seeds which were firm and resistant to gentle pressure were assumed to be viable (Roberts and Ricketts 1979).

The total numbers of sound seeds extracted from the July and November sets of soil cores were summed. For each collection the number of seeds/ m^2 for each species was calculated. The expected composition of the seed bank at its lowest and highest levels was also calculated. The lowest level of the seed bank, representing midsummer, was calculated by taking the number of sound seeds of each species in the predicted seed rain from the previous year and multiplying them by the percent of viable seeds which were ungerminated for that species after the spring flush of germination. The highest level of the seed bank, representing late autumn, was calculated by multiplying the number of sound seeds of each species in the expected seed rain by the percent of post-stratification germination for that species

and adding that number to the number of seeds of that species which were expected to be present in the midsummer seed bank. For each collection date the number of seeds/m² for each species was calculated. The expected numbers of seeds/m² were then compared to the observed numbers of seeds per square meter by means of a chi-square test for goodness of fit. According to Sokal and Rohlf (1981), for a chi-square test for goodness of fit to be considered legitimate, the smallest expected value should be 5 or greater. In the case of both the predicted summer and the predicted winter seedbanks, several species had expected numbers of seeds/m² which were less than 5. These species were therefore classified together as "others" to create a class with a sufficiently large expected value for analysis.

4.3 Results

Predispersal seed viability

The cumulative germination curves of the biennials are given in Figure 4.2. Seeds of *Alliaria petiolata* failed to germinate, thus this species is not included in Figure 4.2. These curves indicate that the biennial species could be divided into 5 groups on the basis of their germination behavior. Group 1 consisted of species which did not have an after-ripening requirement (Figure 4.2 a-f). Nearly all of the seeds which germinated did so within 10 days of being placed in the incubator and stratification had virtually no effect on those seeds which failed to germinate. Group 2 consisted of species which had an after-ripening requirement (Figure 4.2 g and h). This requirement was more pronounced in *Tragopogon dubius* than in *Tragopogon pratensis*. Once the after-ripening requirement had been met, virtually all

Figure 4.2. Cumulative mean percent germination of freshly ripened seeds of 15 biennial species in a controlled environment. Bars represent ± 1 S.D.. The break in the cumulative germination curve represents a period of stratification. See text for explanation of treatment conditions.

a (upper left) *Dipsacus sylvestris*

b (upper right) *Arctium minus*

c (lower left) *Verbascum blattaria*

d (lower right) *Verbascum thapsus*

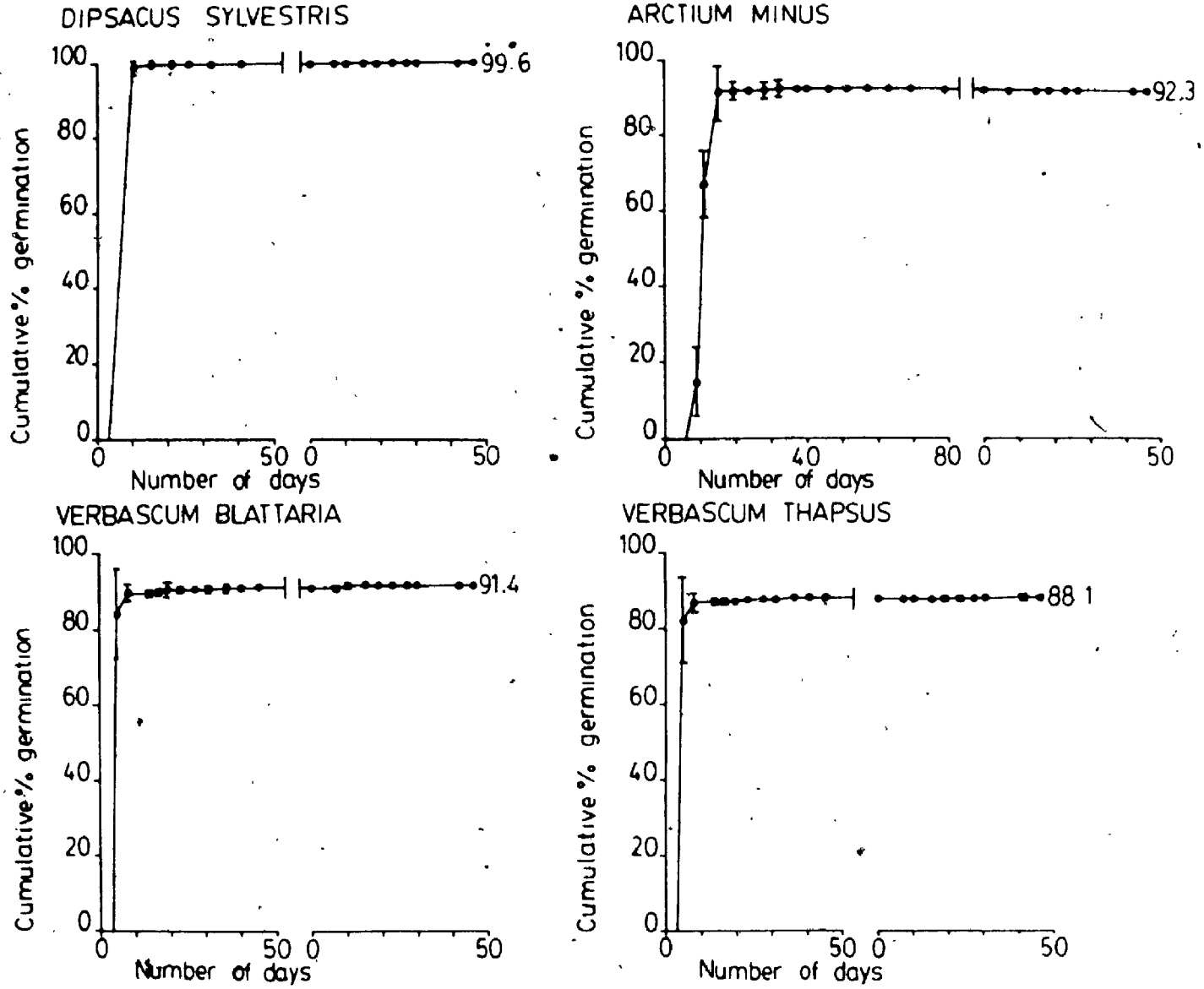

DIPSACUS SYLVESTRIS
ARCTIUM MINUS
VERBASCUM BLATTARIA
VERBASCUM THAPSUS
Cumulative % germination
Number of days
99.6
92.3
91.4
88.1
0
20
40
60
80
100
50
80

Figure 4.2. Continued.

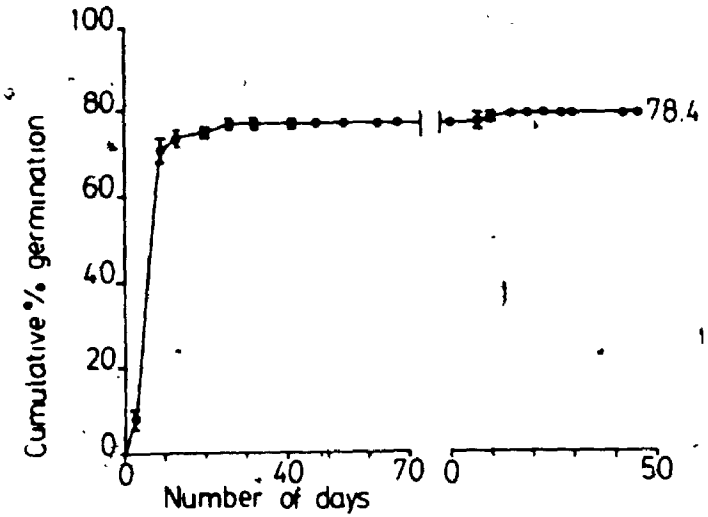
e (upper left) *Cirsium vulgare*

f (upper right) *Lactuca scariola*

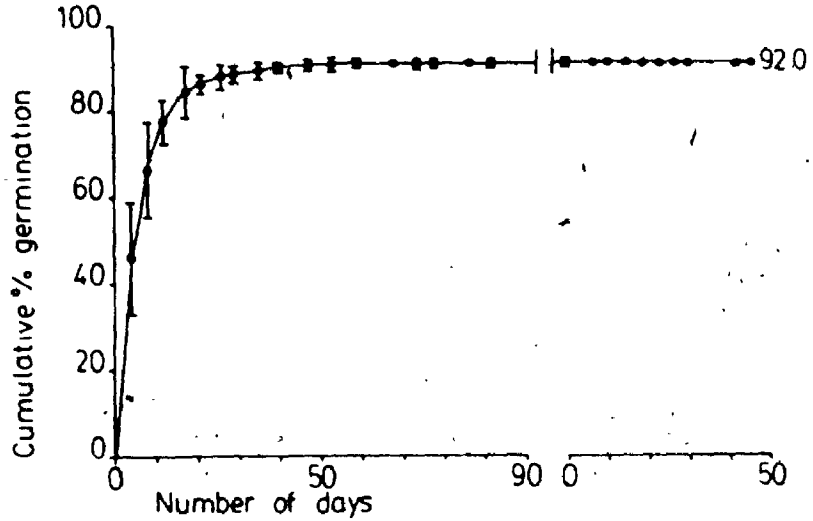
g (lower left) *Tragopogon dubius*

h (lower right) *Tragopogon pratensis*

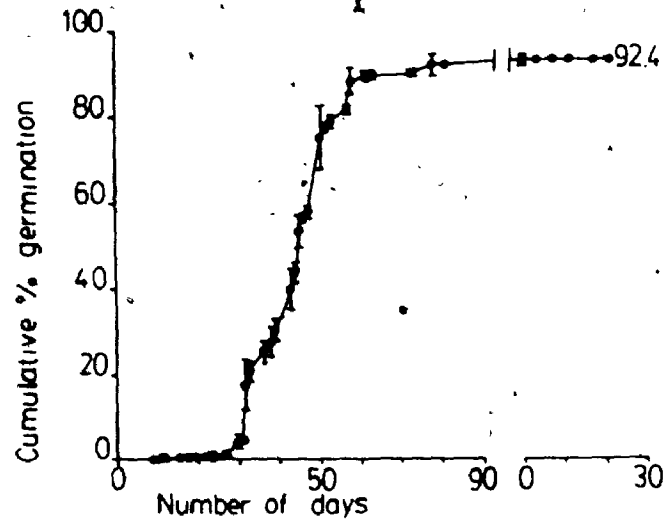
CIRSIUM VULGARE



LACTUCA SERRIOLA



TRAGOPOGON DUBIUS



TRAGOPOGON PRATENSIS

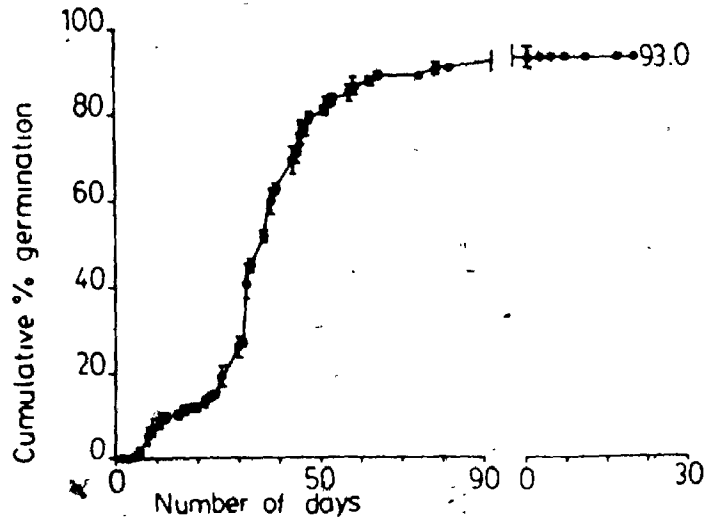


Figure 4.2. Continued.

i (upper left) *Oenothera biennis*

j (upper right) *Daucus carota*

k (lower left) *Melilotus alba*

l (lower right) *Echium vulgare*

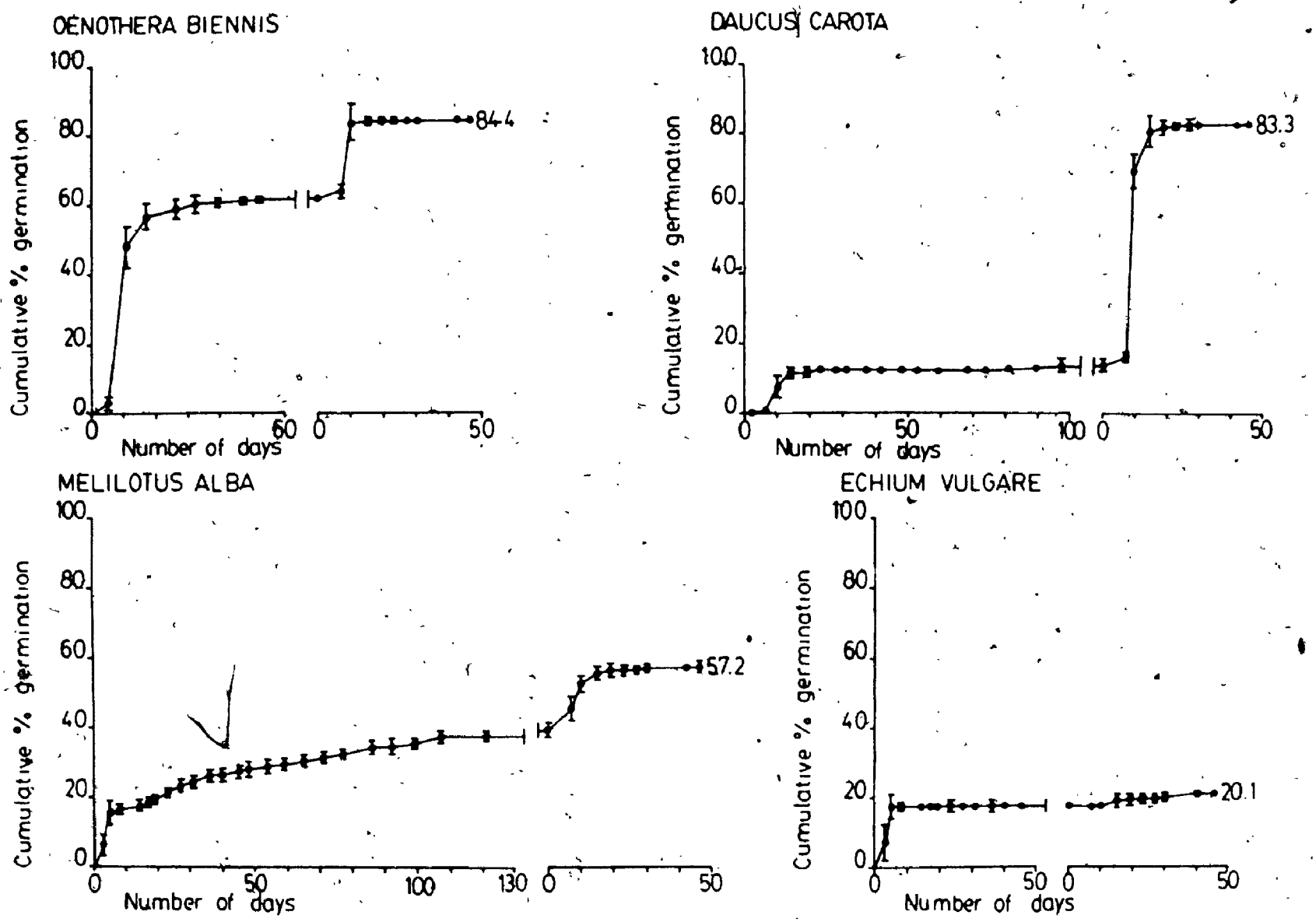
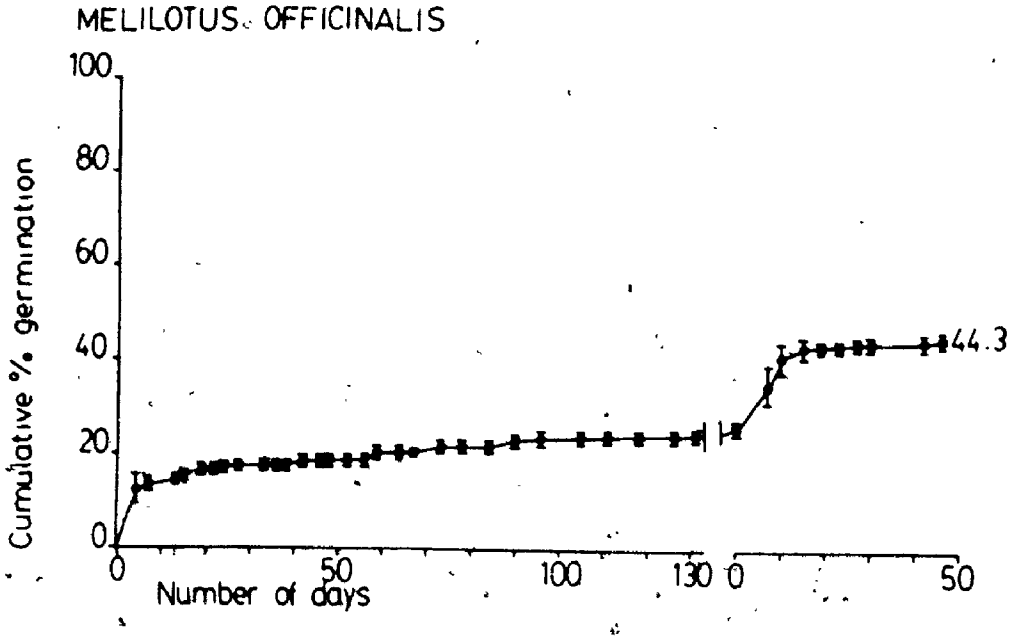
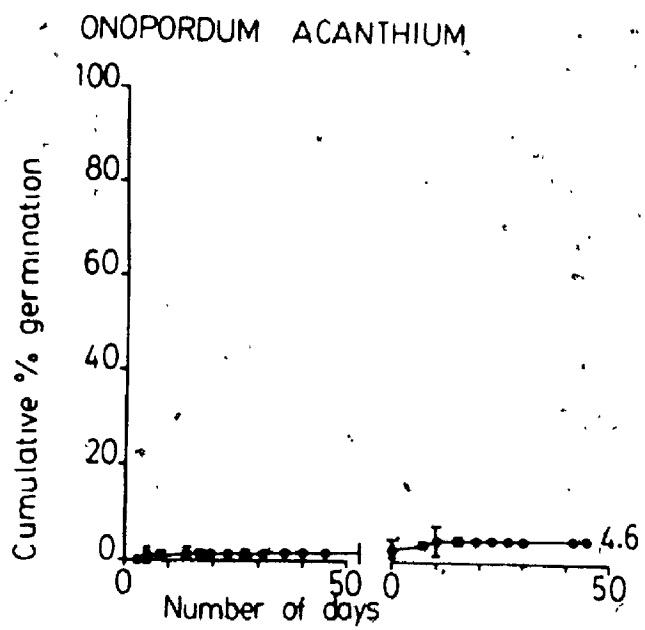

OENOTHERA BIENNIS
Cumulative % germination
100
80
60
40
20
0
0
60
0
50
Number of days
84.4
DAUCUS CAROTA
Cumulative % germination
100
80
60
40
20
0
0
50
100
0
50
Number of days
83.3
MELILOTUS ALBA
Cumulative % germination
100
80
60
40
20
0
0
50
100
130
0
50
Number of days
57.2
ECHIUM VULGARE
Cumulative % germination
100
80
60
40
20
0
0
50
0
50
Number of days
20.1

Figure 4.2. Continued.

m (left) *Melilotus officinalis*

n (right) *Onopordum acanthium*


MELILOTUS OFFICINALIS
Cumulative % germination
100
80
60
40
20
0
0
50
100
130
0
50
Number of days
44.3


ONOPORDUM ACANTHIUM
Cumulative % germination
100
80
60
40
20
0
0
50
0
50
Number of days
4.6

of the seeds which germinated did so within 30 days and stratification failed to induce germination in any seeds which had not germinated. Group 3 consisted of species in which a proportion of the seeds were capable of germination immediately upon harvest, but the remainder required stratification before they could germinate (Figure 4.2 i and j). *Oenothera biennis* had the greater proportion of its seeds able to germinate before stratification whereas the greater proportion of *Daucus carota* seeds were only able to germinate after stratification. Group 4 consisted of species which germinated gradually and continously throughout the entire study period (Figure 4.2 k and m). For both *Melilotus* species a few seeds were capable of immediate germination. Subsequent germination of seeds of both species was staggered throughout the study period. Stratification had a mild promotive effect on germination in both species, but many seeds still had not germinated by the end of the study period. Group 5 was made up of species which had few seeds capable of germination under the incubation conditions provided in this study (Figure 4.2 l and n). A small percentage of *Echium vulgare* seeds were able to germinate initially but few others germinated. The period of stratification had a slight promotive effect on seeds of *Onopordum acanthium* but overall few seeds of this species germinated.

The germination behavior of freshly harvested seeds of the biennials is described in Table 4.1. In each of the four categories (pre-stratification germination, post-stratification germination, viable seeds which did not germinate, and percentage of all seeds which were viable) the F-ratio was highly significant ($P<0.0001$). There were 7 species, *Dipsacus sylvestris*,

Species	Pre-Stratification Germination	Post-Stratification Germination	Failed to Germinate	Percent Viable
Alliaria petiolata	0.0 ± 0.0 h	0.0 ± 0.0 e	100.0 ± 0.0 a	72.4 ± 38.6 b
Arctium minus	99.7 ± 0.5 a	0.0 ± 0.0 e	0.3 ± 0.5 gh	92.6 ± 2.0 ab
Cirsium vulgare	94.5 ± 2.1 b	2.5 ± 1.3 cd	3.0 ± 1.7 f	80.8 ± 5.6 b
Daucus carota	16.6 ± 4.8 f	81.7 ± 5.6 a	1.7 ± 1.5 fg	84.7 ± 4.3 ab
Dipsacus sylvestris	100.0 ± 0.0 a	0.0 ± 0.0 e	0.0 ± 0.0 h	99.6 ± 1.0 a
Echium vulgare	18.5 ± 5.5 f	2.4 ± 3.6 cde	79.1 ± 6.3 c	96.0 ± 3.6 ab
Lactuca scariola	99.6 ± 0.8 a	0.4 ± 0.8 e	0.0 ± 0.0 h	92.0 ± 5.8 ab
Melilotus alba	50.2 ± 6.5 d	26.4 ± 6.1 b	23.4 ± 6.0 e	74.8 ± 5.0 b
Melilotus officinalis	28.5 ± 5.4 e	23.8 ± 5.4 b	47.6 ± 7.7 d	84.9 ± 5.4 ab
Oenothera biennis	72.2 ± 5.8 c	26.9 ± 6.4 b	0.8 ± 1.0 gh	85.1 ± 4.9 ab
Onopordum acanthium	2.4 ± 2.4 g	6.0 ± 6.2 c	91.5 ± 6.7 b	72.2 ± 31.1 b
Tragopogon dubius	99.2 ± 2.0 a	0.8 ± 2.0 de	0.0 ± 0.0 h	92.4 ± 7.5 ab
Tragopogon pratensis	97.4 ± 5.1 a	2.6 ± 5.1 de	0.0 ± 0.0 h	93.0 ± 5.8 ab
Verbascum blattaria	99.5 ± 1.2 a	0.4 ± 0.8 e	0.1 ± 0.4 h	91.5 ± 8.5 ab
Verbascum thapsus	99.4 ± 0.8 a	0.3 ± 0.7 e	0.2 ± 0.5 h	88.4 ± 6.8 ab

Table 4.1. Patterns of seed germination behavior in a controlled environment expressed as a mean (± S.D.) percentage of the viable seeds of each of 15 biennial species. See text for explanation of treatment conditions.

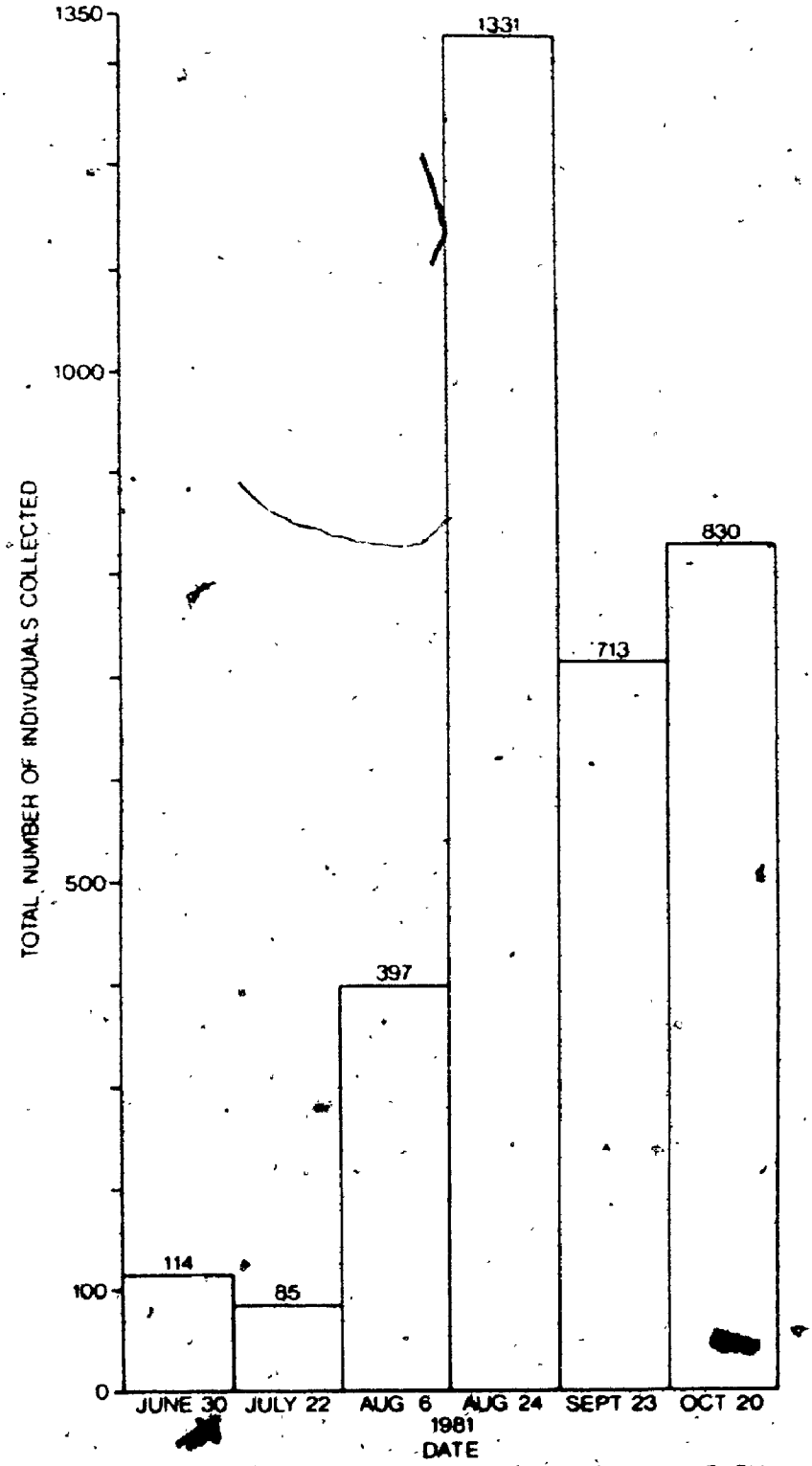
Arctium minus, *Verbascum thapsus*, *Verbascum blattaria*, *Tragopogon dubius*, *Tragopogon pratensis*, and *Lactuca scariola*, which had greater than 97.0% of their viable seeds capable of germination before stratification. The remaining 8 species were variable, ranging from 94.5% to 0.0%. Only in one species, *Daucus carota*, was a large percentage of the remaining viable seeds able to germinate after stratification. Three species, *Melilotus alba*, *Melilotus officinalis*, and *Oenothera biennis*, had approximately 25% of their remaining viable seeds able to germinate after stratification. All other species were somewhat variable, but had 6% or less of their seeds capable of germination after stratification.

The percentage of viable seeds which failed to germinate was also variable among the biennial species. *Alliaria petiolata*, *Echium vulgare*, and *Onopordum acanthium* each had a substantial portion of their viable seeds remain dormant. *Melilotus alba* and *Melilotus officinalis* had from 25 to 50% respectively of their viable seeds remain dormant. The remaining 10 species had very few dormant seeds. The percentage of viable seeds in the seed crop proved to be a constant trait among the biennial species. *Dipsacus sylvestris* had significantly greater seed viability than the remaining 14 species, but none of the other species were different from any another.

B. Seed rain

The numbers of seeds collected during the study period are presented in Figure 4.3. The small numbers captured in June and July represent the loss of immature fruits of the current season and fruits from the previous season still attached to old flower stalks. Consequently, the collections from

Figure 4.3. Total numbers of diaspores of 15 biennial species collected in an array of seed traps in the Marshall pit during each of 6 sampling periods.



TOTAL NUMBER OF PROPAGULES COLLECTED ON EACH SAMPLING DATE

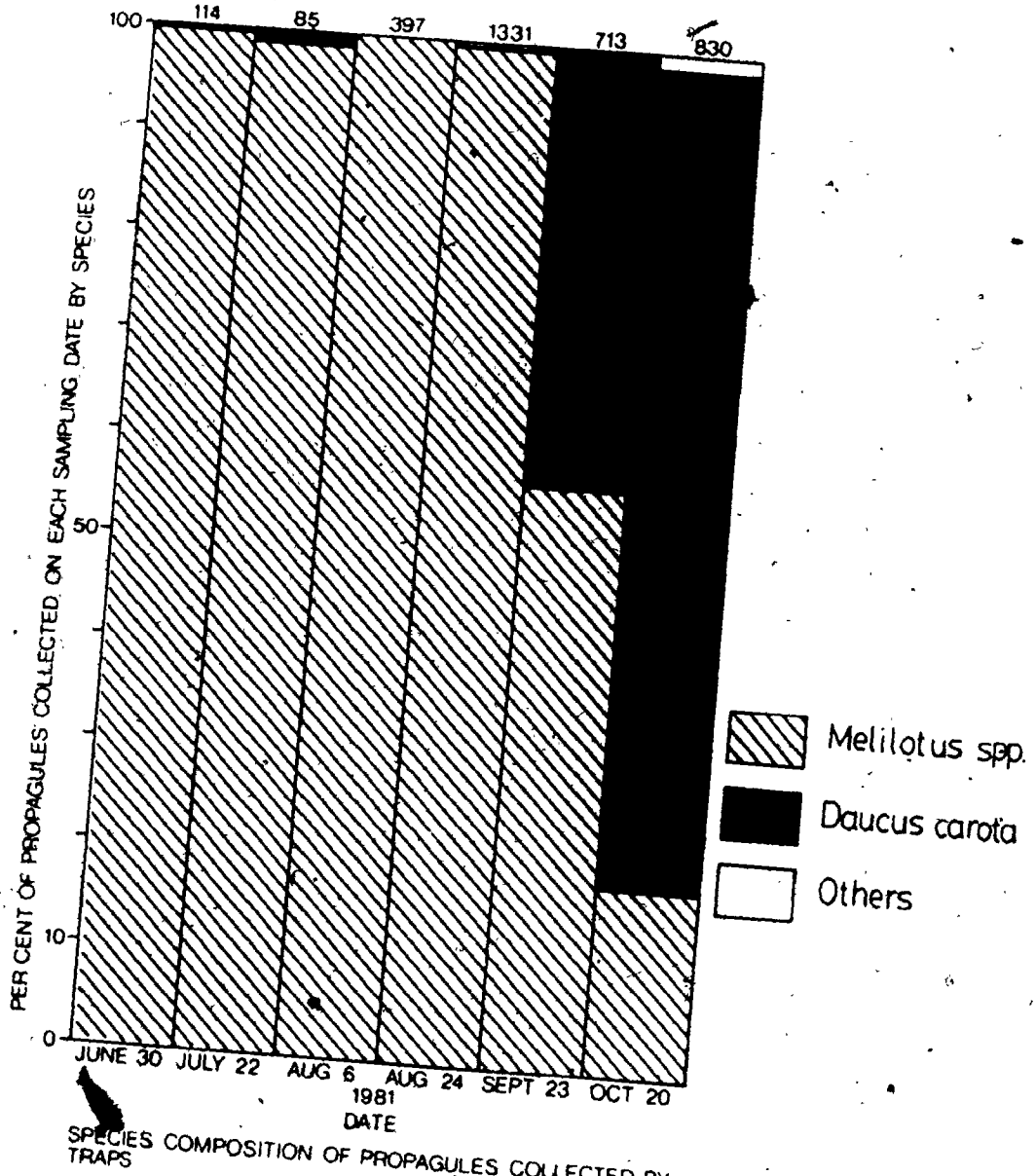
June and July were not used in calculating the expected seed rain for 1981. The numbers of individuals in the seed rain increased from mid-summer to a peak in late August and then declined throughout late summer and fall.

The composition of the seed rain on each collecting date is presented in Figure 4.4. *Daucus carota*, *Melilotus alba* and *Melilotus officinalis* contributed an overwhelming proportion of propagules to the biennial seed rain. Seeds of *Melilotus alba* and *Melilotus officinalis* made up virtually 100% of the biennial seed rain through late August. In September *Daucus carota* made up nearly 50% of the biennial seed rain, and by late October it contributed more than 80%. No other species made a sizeable contribution. Some few fruits of both *Melilotus* species and of *Daucus carota* remained attached to dead flower stalks over winter. Such fruits were the major contributors to seed collections in June and July of 1981.

The estimated composition of the 1981 biennial seed rain is presented in Table 4.2. This estimate reflects the numerical dominance of individuals of *Daucus carota* and both *Melilotus* species in the vegetation of the study area (Table 2.2).

Table 4.3 presents the observed composition of the 1981 biennial seed rain. The two *Melilotus* species and *Daucus carota* provide 99.6% of the seed rain. Table 4.4 presents the result of the chi-square test for goodness of fit for the expected versus the observed seed rain. The predicted biennial seed rain was different from the observed biennial seed rain. Eight taxa, *Cirsium vulgare*, *Daucus carota*, *Echium vulgare*, *Lactuca scariola*, *Melilotus*

Figure 4.4. Species composition of diaspores of 15 biennial species collected in an array of seed traps in the Marshall pit during each of 6 sampling periods.



SPECIES COMPOSITION OF PROPAGULES COLLECTED BY TRAPS

Species	Numbers of m² in Study Area Containing at Least One Flowering Plant	Projected Reproductive Outputs	Estimated Numbers of Viable Seeds	Estimated Numbers of Viable Seeds/m²
Alliaria petiolata	0	0.0	0.0	---
Arctium minus	6	23,107.2	21,397.3	8.1
Cirsium vulgare	30	277,965.0	224,595.7	84.8
Daucus carota	1903	5,548,577.1	4,699,644.8	1,773.4
Dipsacus sylvestris	0	0.0	0.0	---
Echium vulgare	38	179,569.0	172,386.2	65.0
Lactuca scariola	120	330,120.0	303,710.4	114.6
Melilotus alba	1866	18,122,779.0	13,555,839.0	5,115.4
Melilotus officinalis	769	3,971,731.2	3,371,999.8	1,272.4
Oenothera biennis	462	955,138.8	812,823.1	306.7
Onopordum acanthium	43	102,821.6	74,237.2	28.0
Tragopogon dubius	157	19,515.1	18,032.0	6.8
Tragopogon pratensis	0	0.0	0.0	---
Verbascum blattaria	3	22,499.7	20,587.2	7.8
Verbascum thapsus	14	313,945.8	227,528.1	85.8
Total	5411	29,867,769.0	23,552,781.0	8,868.8

Table 4.2. Estimated composition of the rain of diaspores of 15 biennial species within the study area in the Marshall pit during 1981. See text for explanation of methods employed.

Species	Number of Diaspores Collected	Number of Diaspores/m²
Alliaria petiolata	---	---
Arctium minus	---	---
Cirsium vulgare	1	1.2
Daucus carota	948	1149.1
Dipsacus sylvestris	---	---
Echium vulgare	---	---
Lactuca scariola	---	---
Melilotus spp.	2514	3063.4
Oenothera biennis	3	3.6
Onopordum acanthium	8	9.8
Tragopogon dubius	---	---
Tragopogon pratensis	---	---
Verbascum blattaria	---	---
Verbascum thapsus	1	1.2
Total	3470	4228.3

Table 4.3. Actual numbers of diaspores of 15 biennial species which were collected in an array of seed traps within the study area in the Marshall pit in 1981.

Species	Observed Number of Diaspores/m²	Predicted Number of Diaspores/m²	χ^2
Arctium minus	---	8.1	8.1
Cirsium vulgare	1.2	84.8	82.4***
Daucus carota	1149.1	1773.4	220.8***
Echium vulgare	---	65.0	65.0***
Lactuca scariola	---	114.6	114.6***
Melilotus alba	3063.4	5115.4	1730.1***
Melilotus officinalis		1272.4	
Oenothera biennis	3.6	306.7	299.5***
Onopordum acanthium	9.8	28.0	11.8
Tragopogon dubius	---	6.8	6.8
Verbascum blattaria	---	7.8	7.8
Verbascum thapsus	1.2	85.8	81.4***
Total	4228.3	8868.8	2630.3***

*** = significant at P<0.001

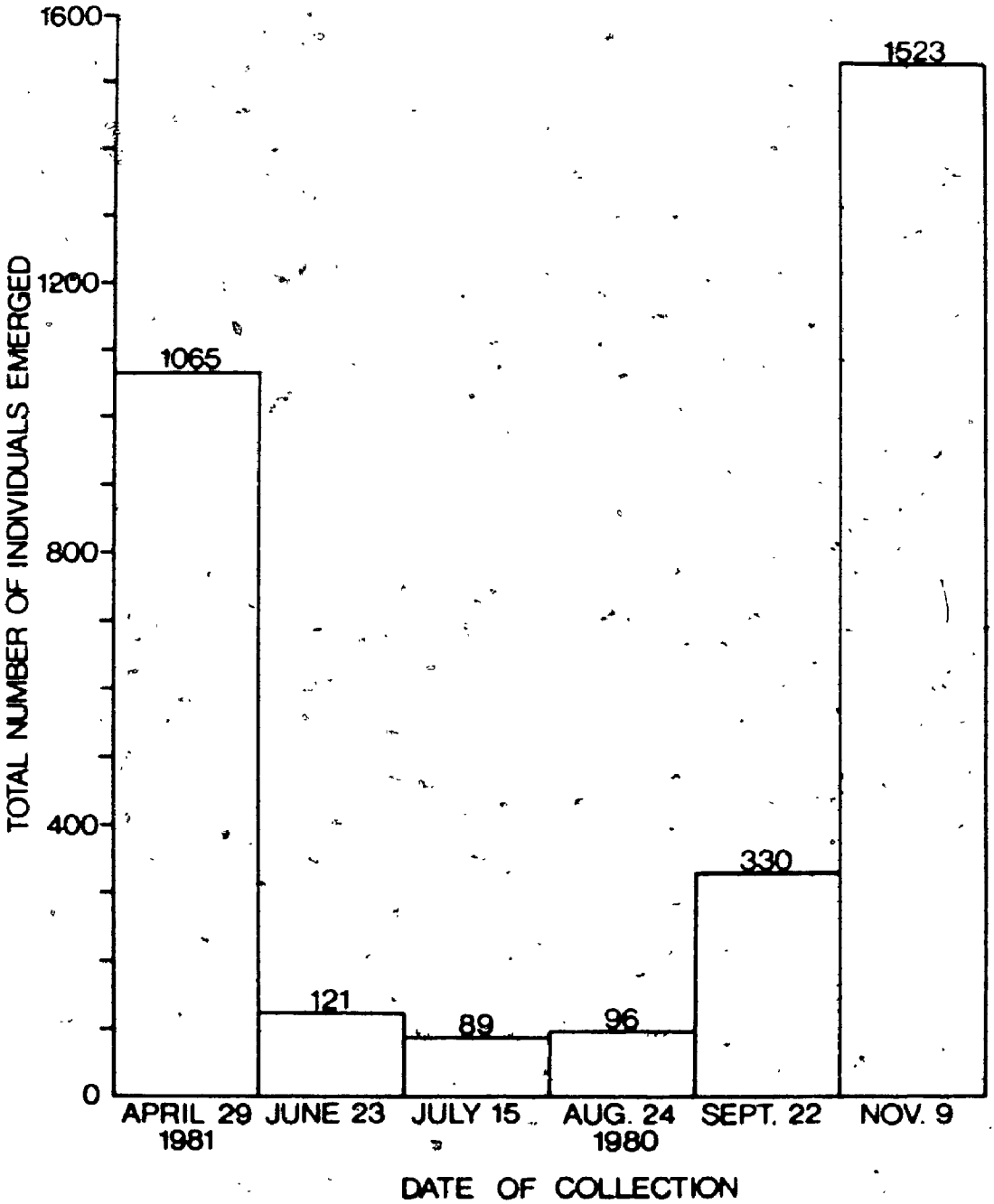
Table 4.4. Comparison of estimated rain of diaspores of 12 biennial species within the study area in the Marshall pit in 1981 with the actual numbers of diaspores of those species collected in an array of seed traps in the study area in the Marshall pit in 1981. Because diaspores of the two *Melilotus* species were indistinguishable, they were grouped as *Melilotus* spp. in the observed seed rain. In the table this value is presented on a line between those for the individual *Melilotus* species.

spp., *Oenothera biennis*, and *Verbascum thapsus*, had significantly ($P<0.001$) fewer seeds present than were predicted. The density of seeds of all biennial species in the 1981 seed rain was found to be 4228.3 seeds/m^2 as compared to an expected value of 8868.8 seeds/m^2.

C. Seed bank

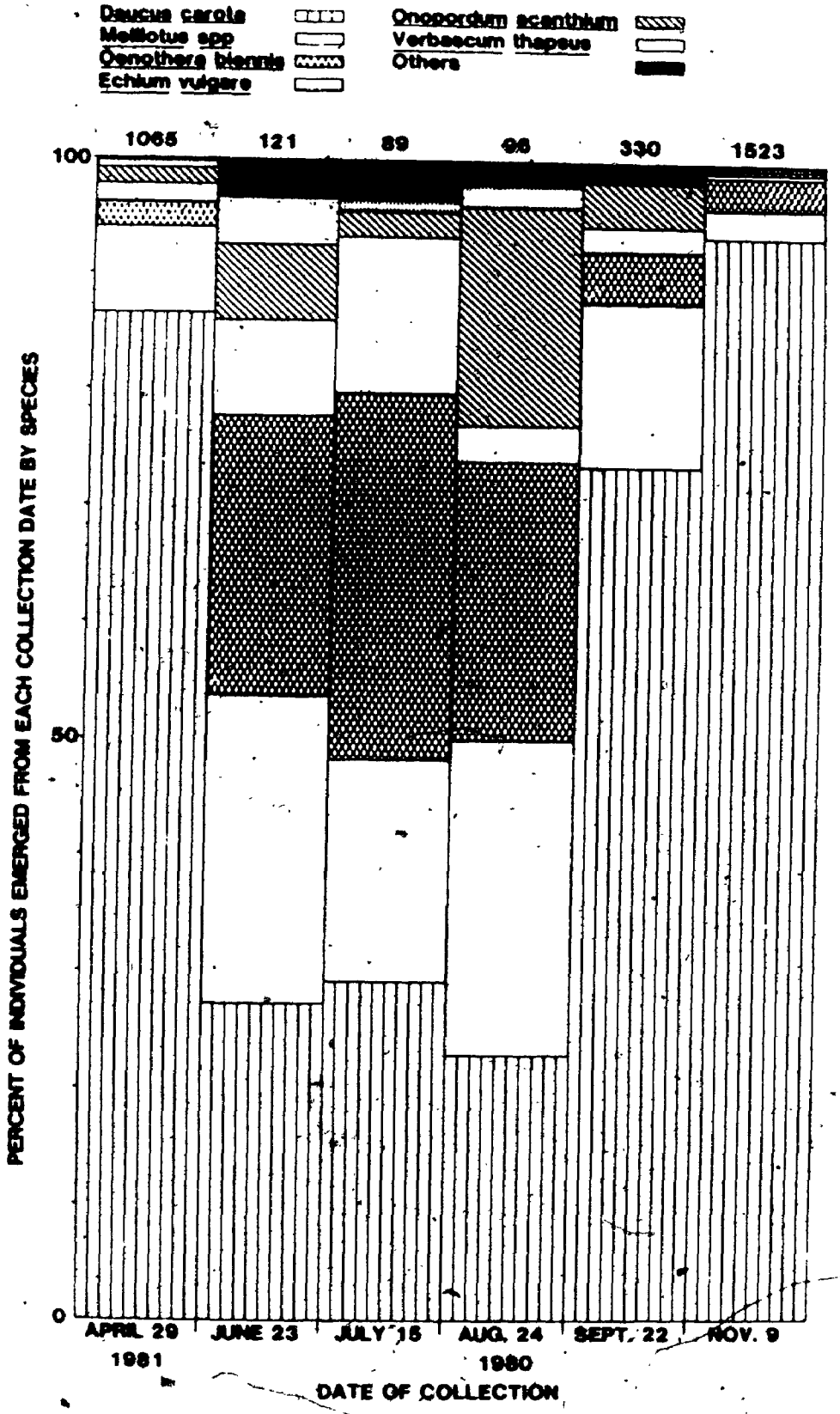
The numbers of seeds (based on emerging seedlings) of biennial species present in the seed bank during the study period are presented in Figure 4.5. The numbers of individuals in the seed bank reached its highest level in late autumn, declined by spring and dropped to its lowest point in mid-summer. The composition of the seed bank on each collecting date is presented in Figure 4.6. *Daucus carota* contributed more than 70% of the biennial seed bank in late September, late November and late April. The increase in the size of the biennial seed bank during these collection dates was caused by the large numbers of *Daucus carota* seeds entering it. While *Daucus carota* seeds contributed less than 30% to the relatively small seed bank which was present during the summer months, seeds of this species were present in the seed bank year round. The decrease in overall size of the biennial seed bank during June, July, and August was caused by individuals of *Daucus carota* leaving the seed bank. Seeds of *Oenothera biennis*, *Melilotus alba*, *Melilotus officinalis*, *Echium vulgare*, *Onopordum acanthium* and *Verbascum thapsus* were also present in the seed bank throughout the year. While the numbers of seeds of these species in the seed bank showed some seasonal flux, the overall sizes of their seed banks were more consistent than that of *Daucus carota*. This is evidenced by their

Figure 4.5. Total numbers of seedlings of 15 bienhial species which emerged from sets of soil cores collected in the Marshall pit during each of 6 sampling periods. Note that all dates of collection were in 1980 except for April 1981.



TOTAL NUMBER OF SEEDLINGS EMERGED FROM EACH SET OF SOIL CORES

Figure 4.6. Species composition of seedlings of 15 biennial species which emerged from sets of soil cores collected in the Marshall pit during each of 6 sampling periods.


Daucus carota
Melilotus spp
Oenothera biennis
Echium vulgare
Onopordum acanthium
Verbascum thapsus
Others
1065
121
89
98
330
1523
100
50
0
PERCENT OF INDIVIDUALS EMERGED FROM EACH COLLECTION DATE BY SPECIES
APRIL 29
1981
JUNE 23
JULY 15
AUG. 24
1980
SEPT. 22
NOV. 9
DATE OF COLLECTION

relatively larger contributions to the total seed bank in mid-summer when *Daucus carota* numbers were lowest, and their relatively smaller contributions in the fall and spring when large numbers of *Daucus carota* seeds were present. No other species was present in the seed bank throughout the year or was present in large numbers during any part of the year.

In Table 4.5 the expected composition of the seed bank in winter is compared with the composition of the seed bank observed in the study area in November 1981. The observed seed bank contained 86.7% *Daucus carota* and 9.5% *Melilotus* spp.. This is significantly different ($P<0.001$) in each case from the prediction that *Daucus carota* would provide 29% and the two *Melilotus* species would provide 67.7% of the seed bank respectively. Two additional species, *Verbascum thapsus* ($P>0.001$) and *Oenothera biennis* ($P>0.05$) had significantly greater numbers of seeds present than were predicted, whereas *Echium vulgare* had significantly ($P<0.05$) fewer seeds present than was predicted.

In Table 4.6 the expected composition of the biennial seed bank at mid-summer is compared with the composition of the seed bank observed in the study area in July 1981. The observed seed bank contained 27.8% *Daucus carota*, 21.9% *Oenothera biennis*, and 17.5% *Melilotus* spp.. This was significantly different ($P<0.001$) in each case from the prediction that the two *Melilotus* species would contribute 94% of the seed bank during mid-summer. In addition, there were significantly more ($P<0.001$) seeds of *Verbascum thapsus* present than were predicted.

Species	Observed Composition of Seed bank on 11/9/81: Numbers of Sound Seeds in Seed bank	Observed Composition of Seed bank on 11/9/81: Numbers of Sound Seeds/m²	Estimated Composition of Seed bank in Winter: Numbers of Seeds in Seed bank	Estimated Composition of Seed bank in Winter: Numbers of Seeds/m²	χ^2
Daucus carota	1,637	4,357.5	3,919,503.8	1,479.0	5,602.3***
Echium vulgare	8	21.3	140,494.8	53.0	19.0*
Melilotus alba	179	476.5	6,750,807.8	2,547.5	2,568.7***
Melilotus officinalis			2,407,607.9	908.5	
Oenothera biennis	49	130.4	225,152.0	85.0	24.2*
Onopordum acanthium	10	26.6	72,381.2	27.3	<0.1
Others	4	10.6	15,266.4	5.9	209.4***
Total	1,887	5,023.0	13,531,214.0	5,106.6	8,423.5***

*** = significant at P<0.001
* = significant at P<0.05

Table 4.5. Comparison of the estimated composition of the seed bank of 15 biennial species in the study area in the Marshall pit in winter with that observed in November 1981. It should be noted that entries which present numbers of seeds/m² represent the numbers of seeds/m² to a depth of 7cm. The significant difference in the Others category is the result of a greater number of seeds of *Verbascum thapsus* being present than was predicted. Because seeds of the two *Melilotus* species were indistinguishable, they were grouped as *Melilotus* spp. in the observed seed bank. In the table this value is presented on a line between those for the individual *Melilotus* species.

Species	Observed Composition of Seed bank on 7/15/81: Numbers of Sound Seeds in Seed bank	Observed Composition of Seed bank on 7/15/81: Numbers of Sound Seeds/m²	Estimated Composition of Seed bank in Summer: Numbers of Seeds in Seed bank	Estimated Composition of Seed bank in Summer: Numbers of Seeds/m²	χ^2
Daucus carota	27	71.1	79,894.0	30.1	55.8***
Echium vulgare	12	31.9	136,357.5	51.4	7.4
Melilotus alba	17	45.2	3,172,066.3	1,197.0	1,713.4***
Melilotus officinalis			1,605,071.9	605.7	
Onopordum acanthium	3	8.0	67,927.0	25.6	12.1
Others	38	101.2	13,880.3	5.3	2362.8***
Total	97	258.2	5,075,196.9	1,914.9	4,151.2***

*** = significant at P<0.001

Table 4.6. Comparison of the estimated composition of the seed bank of 15 biennial species in the study area in the Marshall pit in mid-summer with that observed in July 1981. It should be noted that entries which present numbers of seeds/m² represent the numbers of seeds/m² to a depth of 7cm. The significant difference in the Others category is the result of a greater number of seeds of both *Oenothera biennis* and *Verbascum thapsus* being present than was predicted. Because seeds of the two *Melilotus* species were indistinguishable, they were grouped as *Melilotus* spp. in the observed seed bank. In the [redacted] this value is presented on a line between those for the individual *Melilo[redacted]* species.

4.4 Discussion

A. Seed rain

There are no published studies available which investigated the seed rain present within a community in an open, unproductive habitat in a temperate region. The estimated production of 3,989.0 seeds/m² by the biennial species in the study area is similar to the overall figure of 19,726 seeds/m² produced by 30 species in a tall grass prairie in Missouri (Rabinowitz and Rapp 1980), but is 6 times greater than the largest value, 653 seeds/m², reported for a community which had developed at the base of a glacier in Norway (Ryvarden 1971).

As part of an investigation of seed dispersal among the 15 biennial species, I found that virtually all seeds produced by each of them fell near the base of the parent plant (3.3 D.); thus the actual seed rain was composed of areas of high seed density immediately adjacent to flowering stalks, which graded into areas of low seed density at some distance from a flowering stalk. The seed rain as described by the sampling technique used in this study will necessarily reflect the most numerous species in the study area, or any species which had widespread uniform seed dispersal within the study area. This systematic technique was best suited to detecting seasonal fluctuations in the seed rain throughout the entire study area. Care must be taken however, in the interpretation of comparisons of the densities of seeds in this biennial seed rain with seed densities reported from studies designed to investigate the seed shadows of individual species. For example, Gross (1980b) reported the seed rain of *Verbascum thapsus*

in an old field in Michigan to be 180,000 seeds/m² in a study which concentrated on that species. I found that *Verbascum thapsus* produced 1.2 seeds/m² over my study area. If one uses the reproductive output for *Verbascum thapsus* reported in Table 3.2, one plant standing in the center of a 1m x 1m square would produce a seed rain of over 20,000 seeds/m². The difference between this figure and that reported by Gross (1980b) is probably an artifact of the sampling method used.

I found that *Daucus carota*, *Melilotus alba*, and *Melilotus officinalis*, the three most abundant species in the study area (Table 2.2), contributed 99.6% of the seed rain (Figure 4.4). Thus, the seed rain broadly resembled the standing vegetation. This was also found to be the case in a Missouri tall grass prairie where the 9 most common species contributed 92% of the seed rain (Rabinowitz and Rapp 1980).

Melilotus officinalis began to disperse seeds in early August and *Melilotus alba* began to disperse seeds in mid-August (2.2). By the third week in August the seed rain had reached its greatest intensity and the two *Melilotus* species contributed 100% of it (Figure 4.4). *Daucus carota* began to disperse seeds in early September (2.2) and by late September it contributed almost 50% of the seed rain (Figure 4.4). This species continued to disperse seeds throughout autumn (2.2). Its dispersal reached a peak in late November at which time it contributed 85% of the seed rain (Figure 4.4). Seed dispersal of both species of *Melilotus* began to decline in the autumn (2.2). This resulted in an overall reduction in the numbers of seeds present in the seed rain in the study area (Figure 4.3).

All seeds collected in June and July were those of *Daucus carota* and *Melilotus* spp. (Figure 4.4) which had remained attached to dead flower stalks over winter. The number of such seeds is a small percentage of their seed production in any given year. The significance of seeds which overwinter on the dead flower stalks to the long distance dispersal of these species has been discussed in 3.4 D.2. The importance of such seeds to the population dynamics of these species within the study area is uncertain. Based on the small numbers of *Daucus carota* seeds collected before the current crop began to disperse (Figure 4.4), they probably have negligible impact. Dale and Harrison (1966) tested 1,200 seeds which had overwintered on the stalks of *Daucus carota* and only 3 germinated. Seeds of *Melilotus* spp. overwinter on dead flower stalks in greater numbers than do seeds of *Daucus carota*. No data have been published which report the viability of such seeds. Given their impermeable seed coats (Hamly 1932, Salisbury 1961) and their longevity (Crocker 1938), it is probable that a sizable proportion of such seeds are viable. It is possible that the seed rain of *Melilotus* spp. within the study area for any given year contains up to 5% viable seeds from the seed crop of the previous year. The influence on the population dynamics of *Daucus carota*, *Melilotus alba* and *Melilotus officinalis* of such seeds merits further investigation.

B. Germination and dormancy

Laboratory investigations by other people involving each of the 6 species in group 1 (see 4.3 A. for composition of groups), have shown that freshly ripened seeds of these species, given a favorable temperature regime,

can germinate to high percentages immediately after dispersal, 99.7% for *Dipsacus sylvestris* (Werner 1975a); 78% for *Arctium minus* (Grime et al. 1981); 97% for *Verbascum blattaria* (Baskin and Baskin 1981); 97% for *Verbascum thapsus* (Baskin and Baskin 1981); 63% for *Cirsium vulgare* (Grime et al. 1981); and 74% for *Lactuca scariola* (Marks and Prince 1982). These reported cumulative germination percentages are similar to those found in my study (Figure 4.2).

Given their lack of an after-ripening requirement, it would be expected that seeds of group 1 species would germinate to similar percentages in the field after they disperse. However, studies of the germination of these 6 species in natural situations, *Dipsacus sylvestris* (Werner 1975b, Grime et al. 1981), *Arctium minus* (Gross and Werner 1983), *Verbascum blattaria* (Maguire and Overland 1959, Kivilaan 1975, Baskin and Baskin 1981), *Verbascum thapsus* (Gardner 1921, Toole et al. 1957, Maguire and Overland 1959, Semenza et al. 1978, Gross 1980, Grime et al. 1981, Baskin and Baskin 1981, Reinartz 1984b), *Cirsium vulgare* (Salisbury 1961, Roberts and Chancellor 1979, van Leeuwen and van Breeman 1980, Grime et al. 1981), *Lactuca scariola* (Prince et al. 1978, Prince and Marks 1982, Marks and Prince 1982); have shown that seeds of each of them contain a mechanism sensitive to both the intensity and the quality of light that will prevent their germination if they become buried or lodge beneath a foliar canopy. In addition to light-induced dormancy, van Leeuwen (1981) has found that the activity of soil microbes can inhibit germination in seeds of *Cirsium vulgare* in nutrient poor situations. Although a few seeds of each of these 6 species do germinate in the field after dispersal in most years, most of those produced are induced

into a dormant state in which they pass the winter. Each of these species employs what Angevine and Chabot (1979) term a cold avoiding germination syndrome.

Few studies involving the species in group 2 exist. Everson (1949) found that seeds of *Tragopogon* spp. germinated to 90% in the laboratory and had no light requirement, and Steinbauer and Grigsby (1957) found that there was no primary dormancy in *Tragopogon pratensis*. The available reports from the literature support the findings of my study that neither of these species has dormant seeds. The germination behavior of both *Tragopogon* species fits into what Angevine and Chabot (1979) have termed a drought-avoidance syndrome. Both species shed seeds in mid-summer (2.2), seeds in the seedbank undergo a period of after-ripening under high summer temperatures when moisture availability tends to be low (Figure 4.2 g and h). Their seedlings emerge in late summer when environmental conditions are more favorable.

Both *Tragopogon* species overwinter in the Marshall pit as rosettes rather than as dormant seeds. Reports from the literature indicate that seeds of *Tragopogon dubius* in Saskatchewan mostly germinate during the spring after their dispersal (Chepil 1946) and that those of *Tragopogon pratensis* germinate to 100% the spring after their dispersal in Denmark (Dorph-Peterson 1925). These studies were carried out in areas with shorter growing seasons than that of my study, so the only relevant information to be gained from them is that neither species of *Tragopogon* forms a seed bank which persists for as long as a year.

Species in group 3 employ a germination behavior which Angevine and Chabot (1979) have termed a cold-avoiding syndrome. Laboratory studies involving these species have shown that some of the seeds of these species are capable of germination immediately upon harvest, 70% for *Oenothera biennis* (Steiner 1968), and 34% (Grime *et al* 1981), 30% (Lacey 1982), or 1% (Dale and Harrison 1966) for *Daucus carota*. The remainder of their annual seed crop is innately dormant (*sensu* Harper 1977) and delays germination at least throughout the winter.

Daucus carota has seed dormancy which is mechanical in nature. There is a cap of endosperm which prevents elongation of the radicle (Dale and Harrison 1966). *Oenothera biennis* has dormancy which results from a seed coat effect and an inactive embryo (Gardner 1921).

Both the fall germination pattern of *Daucus carota* reported by Dale and Harrison (1966) and that of *Oenothera biennis* reported by Steiner (1968) closely resemble those of the same species in my study (Figure 4.2 i and j). Field studies however, have shown that seeds of *Oenothera biennis* are sensitive to light when the temperature is favorable for germination (Gardner 1921, Toole et al. 1957, Steiner 1968). Gross (1985) found that seeds of this species required exposure to light for more than 1 hour before they would germinate. She also found that seeds of *Oenothera biennis* were highly sensitive to far-red light (Gross 1985). Seeds of this species which become buried or lodge under a foliar canopy after dispersal do not germinate, but are induced into secondary dormancy.

Although fall germination in the field has been recorded for *Oenothera biennis* (Steiner 1968), probably only a small percentage of recently dispersed seeds do so. An endosperm cap which covers the radicle prevents germination of all but a very small percentage of freshly ripened seeds of *Daucus carota* (Dale and Harrison 1966). Although a portion of any given crop of seeds of this species is sensitive to light (Gardner 1921, Everson 1949, Salisbury 1961, Dale and Harrison 1966, Dale 1974, Grime et al. 1981), and some fall germination has been reported in the field (Martin 1943, Salisbury 1961, Dale and Harrison 1966, Dale 1974, Lacey 1982), the greatest amount of germination occurs in the year after dispersal, beginning in the spring and continuing throughout the growing season.

Laboratory studies have shown that the germination behavior of the species in Group 4 is enforced by the relative impermeability of their seed coats to water ('hardness') (Hamly 1932, Turkington et al. 1978). This germination behavior is also termed a cold-avoiding syndrome by Angevine and Chabot (1979). I found that there was an initial flush of germination of nearly 15% for *Melilotus alba* (Figure 4.2 k) and nearly 10% for *Melilotus officinalis* (Figure 4.2 m). Following this initial flush, germination in both species was intermittent until the beginning of stratification. Following stratification, there was a flush of about 15% germination, but subsequent germination was again intermittent in both species until the termination of the experiment. After the experiment was terminated, 62.5% of the seeds of *Melilotus alba* and 31.6% of those of *Melilotus officinalis* were still viable but had failed to germinate. Salisbury (1961) reported that 25-75% of a given seed crop of *Melilotus alba* could germinate when freshly mature, but that

the remainder remained dormant until their seed coats became permeable. Presumably *Melilotus officinalis*, a closely related species, is similar in this respect.

The germination behavior of both *Melilotus* species should lead to the continous emergence of their seedlings on a seed by seed basis in the field during any time of the year when the temperatures allow it. A flush of emergence should occur immediately after dispersal when the soft-seeded individuals germinate, and another flush should occur in the early spring when all seeds whose coats became permeable during the winter germinate. Turkington et al. 1978) reported that seeds of *Melilotus alba* germinate during any month of the year, including the dead of winter, if there is a thaw of at least three days; but that there are two major peaks of emergence, one in spring, and another in early fall. Gorski et al. (1978) found no evidence of inhibition of germination in seeds of *Melilotus alba* by light passed through foliar canopies, so location of a seed under closed vegetation should not be an obstacle to germination in the field.

Laboratory studies involving species in group 5 have demonstrated that their low germination response is the result of a variety of types of innate dormancy. Seeds of *Onopordum acanthium* contain a water soluble germination inhibitor and are light sensitive (Young and Evans 1969). Possession of a water-soluble germination inhibitor is characteristic of species which employ a drought-avoiding germination syndrome (Angevine and Chabot 1979). The growing season in southwestern Ontario is normally relatively moist (Figure 2.2). Thus, the chemical germination inhibitor should rapidly be leached out of seeds of *Onopordum acanthium* and not be an

important factor in their dormancy in the study area. It has been reported that a percentage of the seeds of this species, 8-14% (Young and Evans 1972), or 28% (Scifres and McCarty 1969), are non-dormant at maturity. The results of my study, 4.6% total cumulative germination (Figure 4.2 n), support the findings of Young and Evans (1972). The innate dormancy present in freshly ripened seeds of *Onopordum acanthium* can be broken, however, by exposure to high alternating temperatures. Seeds of this species have been found to germinate to more than 90% when placed at alternating 35/25C in a controlled environment (M. Steel, E. Sidlo, personal communication). Roberts and Chancellor (1979) reported that there is some fall germination of seeds of *Onopordum acanthium* in the field in Britain. It is unlikely, however, that freshly ripened seeds of this species would encounter sufficiently high temperatures in my study area during late summer to overcome their innate dormancy. Fall germination should be very slight for *Onopordum acanthium* in the Marshall pit.

Both the remaining species in this group had germination behavior which was characteristic of a cold-avoidance syndrome (Angevine and Chabot 1979). Cavers et al. (1979) found that seeds of *Alliaria petiolata* possess a deep innate dormancy. No seeds of this species germinated in any treatment provided by Grime et al. (1981). This correlates with the total absence of germination by this species in my study. In southwestern Ontario, Cavers et al. (1981) reported that no seeds of *Alliaria petiolata* germinate in the field for approximately 1.5 years after their dispersal because of their deep dormancy. However, in more recent studies with different overwintering treatments, large numbers of seeds set into the field just

under the soil germinated after one winter (P.B. Cavers, personal communication). The nature of the seed dormancy present in *Echium vulgare* is uncertain. Grime et al. (1981) have reported that seeds of this species have no light requirement and germinate across a wide range of temperature regimes. Grime et al. (1981) obtained 2% germination from fresh seeds of *Echium vulgare*. The percent germination rose to 12% after stratification (Grime et al. 1981). Van Breeman (1984) found that seeds of *Echium vulgare* germinated rapidly under a wide variety of temperature and soil-moisture conditions. Seeds of this species germinated to the highest percentage, 94.2%, at 30/20C in a 12hr/12hr photoperiod at 6-12% soil moisture (van Breeman 1984). She also found that seeds of *Echium vulgare* had no light requirement for germination. In my study 20% of freshly matured *Echium vulgare* seeds germinated rapidly, but the rest remained dormant throughout the duration of the experiment (Figure 4.2 1). Some seeds of this species germinate in the fall in the field (Salisbury 1961, Klemow and Raynal 1985). The tendency in *Echium vulgare* for seed dormancy not to be broken by stratification indicates both that a relatively small proportion of the seed rain germinates in a given year and that there is the potential for this species to form a large persistent seed bank. Klemow (1982), however, reported that seeds of *Echium vulgare* did not remain dormant in the soil in an abandoned limestone quarry in New York for more than one year.

C. Seed bank

The numbers of seeds of the 15 biennial species which were present in the persistent seed bank in the study area varied greatly between mid-summer and late fall. There were 5,406.8 biennial seeds/m^2 present in November (Table 4.5) but only 255.1 biennial seeds/m^2 present in July (Table 4.6). Both these figures however, fall within the range of densities reported for the seed banks formed by various vegetation types (Silvertown 1982).

Melilotus alba, *Melilotus officinalis*, and *Daucus carota*, the three species which contributed 99.6% of the rain of biennial seeds which fell within the study area (Figure 4.4), also contributed more than 90% of the biennial seed bank which was present in the study area (Figure 4.6). *Oenothera biennis*, *Echium vulgare*, and *Onopordum acanthium*, however, were relatively abundant in the seed bank in mid-summer (Figure 4.6), but were virtually absent from the seed rain (Figure 4.4). Every species present in the seed bank was not necessarily in the seed rain, but the seed bank contained every species present in the seed rain. Rabinowitz (1981) reported a similar situation in a tall grass prairie in Missouri.

The three most abundant species in the biennial seed bank in the study area, *Daucus carota*, *Melilotus alba*, and *Melilotus officinalis*, were also the three most abundant species in its standing vegetation (Table 2.2). In published surveys of seed banks, the species composition of a seed bank has generally been found to be very different from that of the standing vegetation (Roberts 1981, Grime 1979, Harper 1977). In regularly disturbed and in open unproductive habitats however, the seed bank has often been

found to be composed of the same species which are present in the standing vegetation. Wilson et al. (1985) found that in an agricultural system, the three most common weeds contributed 85% of the seed bank whereas Zimmergren (1980), working in an unproductive sandy area in Sweden, found that the seed bank was composed primarily of species present in the plant community.

The estimated compositions of both the mid-summer and late fall biennial seed banks were significantly different ($P<0.001$) from the biennial seed bank compositions observed in the study area in July (Table 4.6) and November (Table 4.5). Underestimation of the expected seed densities for *Oenothera biennis* and *Verbascum thapsus* in both cases resulted because in the field, seeds of both these species were induced into secondary dormancy after dispersal instead of germinating immediately as had been predicted on the basis of their germination behavior in a controlled environment. In both estimated biennial seed banks, the densities of seeds of *Daucus carota* were grossly underestimated whereas those of both *Melilotus* species were grossly overestimated. The expected densities of seeds of *Echium vulgare* were overestimated in the mid-winter biennial seed bank only. The underestimation of the densities of seeds of *Daucus carota* and *Oenothera biennis* probably resulted from a failure to take into account the size of the persistent seed banks of these species which were present in the study area before my investigation began. The gross overestimation of the densities of seeds of both *Melilotus* species was, in all likelihood, the result of high levels of pre-emergence mortality (K. M. Klemow, personal communication). The diurnal temperature fluctuations encountered in the

soil in the study area were probably of sufficient magnitude to cause the strophioles of seeds of both *Melilotus* species to become permeable to water (Hamly 1932). Both Miles (1974) and Grime et al. 1981) have reported similar results from research which involved other hard-seeded legumes. Once their coats became permeable, seeds of these species would germinate regardless of either their depth of burial or the surface environmental conditions. High levels of pre-emergence mortality would be expected to result from such germination behavior.

With the exceptions of *Tragogogon dubius*, *Tragopogon pratensis*, and *Verbascum blattaria*, every biennial species in my study has been reported to form a persistent seed bank, ie: *Alliaria officinalis* (Cavers et al. 1979), *Arctium minus* (Gross et al. 1980, Roberts and Neilson 1981); *Cirsium vulgare* (Champness and Morris 1948, Roberts and Chancellor 1979, van Leeuwen and van Breeman 1980 van Breeman and van Leeuwen 1983, de Jong and Klinkhammer 1986); *Daucus carota* (Champness and Morris 1948, Beckwith 1954, Dale and Harrison 1966, Holt 1972, Dale 1974, Lacey 1982, Verkaar and Schenkeveld 1984a); *Dipsacus sylvestris* (Werner 1975a, Werner 1977); *Echium vulgare* (Salisbury 1961, van Leeuwen and van Breeman 1980); *Lactuca scariola* (Marks and Prince 1982); *Melilotus alba* and *Melilotus officinalis* (Turkington et al. 1978); *Oenothera biennis* (Oosting and Humphreys 1940, Beckwith 1954), *Onopordum acanthium* (Milton 1943, Roberts and Chancellor 1979); *Verbascum thapsus* (Oosting and Humphrey 1942, Dore and Raymond 1943, Gross and Werner 1978, Reinartz 1984b). Given the dormancy characteristics of *Verbascum blattaria* (Kivilaan and Bandurski 1981), it is probable that the lack of reports of seed bank formation by this species

results from a combination of an absence of studies which used it as a test organism and its relatively rare occurrence which kept it from being detected in surveys of seed banks in general

Several investigations have been performed which determined the size of the seed bank formed by a number of my biennial species when they were growing in open unproductive habitats. Klemow (1982) reported that very few seeds of *Echium vulgare* survived in the soil for more than a year in an abandoned limestone quarry in New York. His findings are in direct contradiction to the results of research which demonstrated that this species forms relatively long-lived seed banks in a dune system in the Netherlands. Van Leeuwen and van Breeman (1980) found that 80% of buried seeds of *Echium vulgare* survived in the soil for more than 1 year. Van Breeman (1984) found that after 3 years 15% of seeds of this species buried at 2cm depth, and 75% of those buried at 15cm depth, were still viable. I found that *Echium vulgare* formed a relatively large persistent seed bank in my study area (Figure 4.6, Tables 4.5 and 4.6). My results support the work of van Leeuwen and van Breeman. It is unexpected that this species should have such a different dormancy pattern in a similar habitat less than 400km away from my study site. *Melilotus alba* was reported to form persistent seed banks in an abandoned limestone quarry in New York (Klemow and Raynal 1981). The densities of seeds in these seed banks were estimated to be 9.2 seeds/m^2 in a sparsely vegetated site and 162.0 seeds/m^2 in a densely vegetated site (Klemow and Raynal 1981). In my study *Melilotus alba* and *Melilotus officinalis* were found to form a combined seed bank of 44.7 seeds/m^2 in July (Table 4.6) and 471.0 seeds/m^2 in November (Table 4.5) These densities

are similar to those reported for *Melilotus alba* by Klemow and Raynal (1981). Roberts and Chancellor (1979) created a series of artificial seed banks for *Cirsium vulgare* in Britain. They reported that a very small number of seeds of this species remained viable in the soil for at least 5 years. Van Leeuwen and van Breeman (1980) found that 50% of the seeds of *Cirsium vulgare* which had been buried in a sand dune system in the Netherlands remained viable after 1 year. Van Breeman and van Leeuwen (1983), working in the same habitat found that after 3 years less than 1% of the seeds of *Cirsium vulgare* which had been buried 2cm deep, and 55% of those which had been buried 15cm deep, remained viable. De Jong and Klinkhammer (1986) reported that seed dormancy was not important in the life history of this species in the dune systems in the Netherlands. The results of my study provide additional evidence that *Cirsium vulgare* does not form large persistent seed banks. Roberts and Chancellor (1979) created a series of artificial seed banks for *Onopordum acanthium* in Britain. They reported that after 5 years approximately 7% of the initial seed bank remained viable. I found that this species formed a persistent seed bank in my study area (Figure 4.6). Reinartz (1984b) reported a density of 680 seeds/m² for *Verbascum thapsus* under pine stands in North Carolina. This density is much greater than the 2.6 seeds/m² and 10.5 seeds/m² which I found for this species in the July and November seed banks respectively. The seed bank density of *Verbascum thapsus* reported for my study site might be an artifact of my sampling technique. Flowering stalks of this species are uncommon in the study area (Table 2.2). *Verbascum thapsus* produces a narrow seed shadow around the base of the parent plant (3.4 D.2.). If a soil core was taken by chance very near the spot where a flower stalk of *Verbascum thapsus* had

once stood, my estimation of the density of the seed bank of this species will be high; otherwise it will be low. In all probability, I collected an insufficient number of soil cores to accurately assess the size of the seed bank formed by this species in the study area.

Seven of the biennial species included in my study, *Daucus carota*, *Melilotus alba*, *Melilotus officinalis*, *Oenothera biennis*, *Echium vulgare*, *Onopordum acanthium*, and *Verbascum thapsus*, formed relatively large persistent seed banks in the study area (Figure 4.6). None of the remaining biennial species however, formed a transient seed bank (*sensu* Thompson and Grime 1979) (Figure 4.6). The dynamics of the biennial seed bank in the study area was dominated by *Daucus carota* (Figure 4.6). Large numbers of innately dormant seeds of this species entered the seed bank during the fall, increasing the overall density of seeds from a seasonal low of 255.1 seeds/m^2 (Table 4.6), to a seasonal high of 4965.6 seeds/m^2 (Table 4.5). By November, seeds of *Daucus carota* made up 92% of the seed bank (Figure 4.6). The large numbers of seeds of this species which germinated in spring were responsible for the marked decline in overall numbers which occurred from April to June (Figure 4.5). Some seeds of *Daucus carota* remained in the seed bank throughout the summer, but they contributed only approximately 25% of the seeds present (Figure 4.6). Despite the large numbers of seeds of *Melilotus alba* and *Melilotus officinalis* which were present in the seed rain (Figure 4.4), these species had relatively small seasonal flux in the seed bank (Figure 4.6). Seeds of both species of *Melilotus* had intermittent rather than pulse germination. This behavior resulted in their having relatively stable densities of seeds in the seed bank throughout

the year (Tables 4.5 and 4.6). Consequently, these species comprised a larger proportion of the seed bank in the summer than in fall or spring (Figure 4.6). The remaining four biennials which formed persistent seed banks, *Oenothera biennis*, *Echium vulgare*, *Onopordum acanthium*, and *Verbascum thapsus*, were species which were infrequent in the standing vegetation in the study area (Table 2.2), and which were virtually absent from the seed rain (Figure 4.4). Nevertheless, their seeds, particularly those of *Oenothera biennis*, *Echium vulgare*, and *Onopordum acanthium*, were surprisingly numerous in the seed bank, particularly during the summer. In June, July, and August, seeds of these three species contributed as much as 30 to 40% of the seed bank (Figure 4.6). All four of these species however, have deep seed dormancy and extensive seed longevity. Each year only a small proportion of the seeds they produced were lost to germination or death. Consequently, numbers of their seeds increased in the seed bank each year as long as there was new input.

D. Seed longevity.

In areas of relatively dense vegetation, biennial species exploit a disturbance in the standing vegetation by quickly emerging and establishing, then holding the space they have captured until they are able to set seed (Harper 1977). Seeds of many of these species then remain dormant in the soil until another disturbance creates the opportunity for their emergence and establishment (Harper 1977). In a habitat in which the eventual occurrence of a disturbance is predictable, but its timing is not, this would seem to be a favorable strategy. The Marshall pit is such a

habitat. After the initial devastation of mining, it has remained undisturbed except for small-scale events such as surface erosion, frost heaving, and small animal activity. Thus, the great majority of seeds present in the seed bank in the Marshall pit seem destined for a lengthy entombment before local conditions stimulate them to germinate.

Seed banks decay over time through the germination or death of individual seeds (Harper 1977). In undisturbed plots on abandoned agricultural land Roberts and Dawkins (1967) found that when seed input was prevented, the numbers of viable weed-seeds in the soil declined exponentially by 22% annually. During the first year, 4.5% of the viable seeds in the soil emerged, but by year 4, only 0.3% of the viable seeds were able to emerge; the rest were buried too deep and either died during attempted emergence or remained dormant (Roberts and Dawkins 1967). In another investigation, Roberts and Feast (1973) mixed known numbers of annual weed seeds in soil and prevented further seed input. They reported that the annual exponential rate of decline in numbers of seeds in the seed bank was 12%. After the second year of their study, all of the annual decrease was the result of seed death, not germination (Roberts and Feast 1973).

There are formidable disadvantages for a seed which remains a part of the seed bank for too long. Most of the emergent seedlings in a given year originate from the previous year's seed crop (Harper 1977). There seems to be a decline in the likelihood of a seed germinating which is directly proportional to its length of burial (Harper 1977). Seeds in persistent seed banks in undisturbed vegetation have been shown to have a half-life of approximately 3 years (Roberts and Dawkins 1967). In an experimental

situation, annual weed seeds mixed with soil had a half-life of 6 years in the absence of seed input.(Roberts and Feast 1973).

None of the above-mentioned investigations of seed bank decay have involved biennial species, seeds of many of which have been reported to remain viable for extraordinary lengths of time. Reported seed longevity varies greatly among the biennial species included in my study. Seeds of *Alliaria petiolata* remain viable in the soil for at least 18 months (Cavers et al. 1979). Those of *Arctium minus* are reported to have a viability of from 1 to 3 years (Gross et al. 1980, Roberts and Neilson 1981). Seeds of *Cirsium vulgare* have been found to remain viable for at least 5 years (Roberts and Chancellor 1979, van Leeuwen and van Breeman 1980, van Breeman and van Leeuwen 1983). Reported seed longevity for *Daucus carota* varies widely. Kjaer (1948) found that seeds of this species were viable for up to 10 years, whereas Dorph-Peterson (1925), Gross (1980a), and Lacey (1982) report that its seeds live for less than 3 years in the field. Seeds of *Dipsacus sylvestris* have been found to remain viable in the field for 1 to 2 years (Werner 1975a, Werner 1977). Several studies report that seeds of *Echium vulgare* have a longevity of up to 4 years (Dorph-Peterson 1925, van Leeuwen and van Breeman 1980, van Breeman and van Leeuwen 1983, van Breeman 1984). Although seeds of *Lactuca scariola* have been found to remain viable for at least 5 years, the half-life of a seed bank of this species in the field may be as short as 18 months (Toole and Brown 1946, Marks and Prince 1982). Crocker (1938) reported that one-third of the seeds of both *Melilotus alba* and *Melilotus officinalis* held in storage for 40 years were still viable, and that a few seeds of *Melilotus alba* remained viable after 80 years storage.

Seeds of *Oenothera biennis* have been shown to remain viable in the soil for up to 80 years (Darlington and Steinbauer 1961). *Onopordum acanthium* is reported to have seed longevity of up to 40 years (Toole and Brown 1946, Roberts and Chancellor 1979). Neither seeds of *Tragopogon dubius* (Chepil 1946), nor those of *Tragopogon pratensis* (Dorph-Peterson 1925), remain viable for more than 1 year. Seeds of *Verbascum thapsus* have been reported to have longevity of at least 100 years (Kivilaan and Bandurski 1981). It is possible that the extreme longevities of the seeds of some of these biennial species are translated into a greater resistance to death during burial than has been reported for annual weeds of arable lands. The long-term viability of seeds of these species in a natural situation merits further investigation.

E. Post-dispersal seed predation

Hickman (1979) noted that one of the major gaps in current knowledge of plant population biology is the fate of seeds between dispersal and germination. Sagar and Mortimer (1976) have suggested that predation might be the fate of most seeds which remain on the soil surface. Post-dispersal seed predation, particularly among woody species (see Cavers 1983 and Janzen 1971 for reviews) and within desert communities (see Brown et al. 1979 for review), has been the subject of much research. Few such investigations have been performed within herbaceous communities in temperate regions, but some of these have either involved a number of the biennials which are included in my study or are relevant to my research in another way. Van Breeman (1984) reported that as much as 60% of the seed bank of *Echium vulgare* in a dune system in the Netherlands might fall victim to

predators. Working in the same habitat, de Jong and Klinkhammer (1986) found that as many as 60% of the seeds produced by *Cirsium vulgare* might be eaten after they had been dispersed. Virtually all of these seeds were taken by small rodents; seed predation by birds and insects was found to be negligible in this study (de Jong and Klinkhammer 1986). Mittelbach and Gross (1984) reported that there was appreciable post-dispersal seed predation among *Daucus carota*, *Dipsacus sylvestris*, *Tragopogon dubius*, and *Verbascum thapsus* in an old field in southern Michigan. They found that rates of seed loss were greater in undisturbed vegetation than in adjacent tilled land. In undisturbed vegetation from 3-15% of the seeds of these species were lost from treatments each day (Mittelbach and Gross 1984). In their study, seeds of *Tragopogon dubius*, *Daucus carota*, and *Dipsacus sylvestris* were eaten by deer mice (*Peromyscus maniculatus* Wagner), seeds of *Oenothera biennis* were eaten by unidentified ants, and those of *Verbascum thapsus* were removed by an unidentified agent (Mittelbach and Gross 1984). Beckwith (1954) in a study of animal communities of abandoned fields in southern Michigan found that deer mice, meadow voles (*Microtus pennsylvanicus* Ord.) and jumping mice (*Zapus hudsonius* Zimmerman) fed extensively on a variety of weed seeds in fields during the first few years following their abandonment. Radvanyi (1974), in a study conducted in southwestern Ontario in ruderal vegetation of similar composition to that of my study area, found that smoky shrews (*Sorex cinereus* Miller), short-tailed shrews (*Blarina brevicauda* Say), deer mice, meadow voles, and eastern cottontails (*Sylvilagus floridanus* Allen), seed predators all, were present at a density of 98.8 mammals/ha.

I made no systematic investigation of post-dispersal seed predation. Deer mice, meadow voles, jumping mice and eastern cottontails were observed in the study area however, and there is no reason to doubt that seeds of my biennial species were a part of their diets. The only direct evidence that I have of post-dispersal seed predation in the Marshall pit came during my investigation of seedling emergence and establishment (5.4 B.). I found many seeds of both *Tragopogon* species which had been shelled in a manner characteristic of small rodents (Mittelbach and Gross 1984) in both sparsely and densely vegetated plots in my satellite study area.

Mittelbach and Gross (1984) found in their study that seeds of some species were taken by omnivorous ants. However, there were no ant species nesting in my study area which would be expected to eat more than a negligible number of seeds (G. Umphrey, personal communication).

Neither Mittelbach and Gross (1984) nor Klemow (personal communication) found evidence of seed predation by birds in their respective studies. However, I observed mourning doves (*Zenaida macroura* L.), red-winged blackbirds (*Agelaius phoeniceus* L.), brown-headed cowbirds (*Molothrus ater* Boddaert), American goldfinches *Carduelis tristis* L.), and several species of sparrows in my study area during my investigations. Beckwith (1954) reported that all of these birds are granivorous and that they feed extensively on weed seeds in recently disturbed fields in southern Michigan. There is no reason to doubt that these birds also feed on seeds of my biennial species. Potentially, the combined effect of these seed predators could have a profound influence on the seed population dynamics of the biennial species in this study. Post-dispersal seed predation merits

further investigation in this habitat.

Chapter 5

Seedling Emergence, Survival, and Establishment in the Field

5.1 Introduction

Darwin (1860) noted that in nature all populations increase geometrically, and that this abundant reproduction is counterbalanced by mortality which occurs at some period in the life of the organism, with the result that only a small proportion of the offspring produced survive. Mortality, then, can be seen to limit population size. The 15 biennial species on which this investigation is focused are wholly dependent on seeds for regeneration. Therefore, a knowledge of the timing and intensity of mortality in the life cycles of these species is particularly important in understanding their regeneration.

Many studies (Darwin 1860, Harper 1967, Naylor 1972, Sarukhan and Harper 1973, Sharitz and McCormick 1973, Harper and White 1974, Kawano and Nagai 1975, Werner 1975a, Werner 1975b, Hawthorn and Cavers 1976, Mack 1976, Symonides 1977, King 1977b, Werner 1977, Turkington et al. 1978, Cavers et al. 1979, Baskin and Baskin 1979a,b, van der Meijden and van der Waals-Kooi 1979, Cook 1979, Gross 1980, Schaal 1980, Klemow and Raynal 1981, Silvertown and Dickie 1981, Marks and Prince 1981, Gross and Werner 1982, Verkaar and Schenkeveld 1984a, Young 1984, de Jong and Klinkhammer 1986) have demonstrated that most mortality occurs during the seedling stage of a plant life cycle (but also see Holt 1972, Watkinson 1978, Regehr and

Bazzaz 1979, Schaal 1980, Cavers 1983). Therefore, I expected to find high mortality among seedlings of my biennial species. I wondered, however, whether or not differences in the timing and intensity of seedling mortality existed among these species which could in turn help explain their relative abundance and continued co-existence in the study area.

Toward this end I established a series of permanent plots in each of two contrasting representative types of vegetation in the Marshall pit, introduced equal numbers of seeds of each species into each plot, and monitored the emergence and subsequent fate of each biennial seedling through the subsequent growing season.

5.2 Materials and Methods

A. The study area

I felt that the establishment of permanent plots and subsequent periodic seedling mapping would be destructive to the vegetation in the study area and thus would have a detrimental impact on other studies simultaneously in progress. Therefore, permanent plots for the purpose of investigating the emergence and survival of seedlings of the 15 biennial species were established in a satellite area at the toe of the slope of the eastern wall of the Marshall pit approximately 46m east of the primary study area (2.2 A.). The substrate and vegetation in the satellite area were visually comparable to those of the study area.

B. Experimental design

In June 1981 ten permanent plots 1.0 X 1.0m in size were established arbitrarily in the satellite area. The corners of these plots were marked with 26cm eavestroughing nails driven into the ground such that only 2.5cm of their tops were exposed. These corner nails were used to anchor permanent wooden quadrats on each site. Each quadrat was constructed with 5.0cm wide pieces of 2.0cm thick plywood onto which were strung a 10.0 X 10.0cm grid made with 50 pound test pale blue fluorescent fishing line. Five quadrats were located in areas with less than 10% vegetative cover (henceforth called sparsely vegetated sites) and 5 were located in areas with greater than 95% vegetative cover (henceforth called densely vegetated sites). Within each cover type 3 of 5 quadrats were randomly selected for input of biennial seeds and the remaining 2 were left as controls to assess the potential contribution from existing biennial seed banks. Once the quadrats were in place, all bolting individuals of any of the biennial species under investigation were removed from a 5.0m wide area around the plots to minimize immigration of their propagules into sown plots.

C. Seed input

Three hundred seeds of each of the 15 biennial species were introduced into each of the 6 permanent plots which had been selected for sowing. As seeds became ripe in the field during 1981 they were collected and processed. For each species bulk samples of fruits were collected in the Marshall, West Nissouri, and Hill pits. Once collected, the fruits were kept in dry paper bags at ambient outdoor temperatures until processing could

be completed. This processing of seeds differed according to the nature of the fruits. For *Daucus carota*, *Echium vulgare*, and *Dipsacus sylvestris*, infructescences were pulled apart by hand to separate seeds. The fruits of *Alliaria petiolata*, *Arctium minus*, *Melilotus alba*, *Melilotus officinalis*, *Oenothera biennis*, *Verbascum blattaria*, and *Verbascum thapsus*, were ruptured mechanically to release the seeds. For these 10 species the resultant material was passed through a nest of soil sieves with graded mesh sizes. Seeds were then separated from the residue of the fruits by means of a commercial seed blower. Fruits of *Cirsium vulgare*, *Lactuca scariola*, *Tragopogon pratensis*, and *Tragopogon dubius* were collected and the pappus removed by hand. Once cleaned, seeds were sorted into lots for sowing. Seeds of all species were not introduced into permanent plots at the same time because of the differing phenologies of 4 species. Seeds of the 2 *Tragopogon* species were sown on July 14, 1981; seeds of *Alliaria petiolata* and *Melilotus officinalis* were introduced on September 1, 1981, and seeds of the remaining species were introduced on December 1, 1981. All seeds were sown by hand and an attempt was made to sow the seeds evenly across each 1.0m² plot.

D. Data collection

After the initial input of seeds, censuses of seedling emergence in the six plots were made at regular intervals until November 1982. At each census each seedling which had emerged in a sown plot was counted and marked. Those which emerged in unsown plots were counted, but not marked. Seedlings having horizontal orientation, *Alliaria petiolata*, *Arctium minus*,

Cirsium vulgare, *Dipsacus sylvestris*, *Echium vulgare*, *Lactuca scariola*, and *Onopordum acanthium*, were marked by inserting a toothpick alongside the seedling. Those of *Daucus carota*, *Melilotus* spp., *Tragopogon* spp., *Oenothera biennis*, and *Verbascum* spp. were marked by placing a thin ring of 0.8cm diameter Tygon tubing around the stem. Both toothpicks and rings were color-coded for date of census. The emerged seedlings of the 15 species were counted in the control plots during each census. The fate of each marked seedling was followed through to the end of the subsequent (1982) growing season, at which time all survivors were considered to be successfully established. During this interval, the marker for any seedling which died was removed from the study area.

D. Data analysis

Seedlings of pairs of congeneric species were not distinguished in the field and so *Verbascum blattaria* and *Verbascum thapsus* are grouped as *Verbascum* spp., *Melilotus alba* and *Melilotus officinalis* are grouped as *Melilotus* spp., and *Tragopogon dubius* and *Tragopogon pratensis* are grouped as *Tragopogon* spp.. Prior to statistical analysis, values for mean percent seedling survival were transformed to angular values (Sokal and Rohlf 1981). For both mean seedling emergence and mean percent seedling survival, a one-way ANOVA was performed to look for differences between species response within each cover class. The General Linear Model of the Statistical Analysis System was employed for the ANOVAs (SAS 1982). In any case where the F test was significant ($P<0.05$), Tukey multiple pairwise comparisons of the means were performed using the General Linear Model

of the Statistical Analysis System (SAS 1982). Within each cover class the mean number of seedlings emerged for each taxon was compared with an expected emergence value calculated from the germination behavior of each species in the laboratory (Table 4.1). The procedure employed was a Student's t-test modified for the comparison of a single observation with the mean of a sample (Sokal and Rohlf 1981). For both mean seedling emergence and mean percent seedling survival comparisons were made between cover classes for each taxon. The procedure employed was TTEST from the Statistical Analysis System (SAS 1982).

5.3 Results

A. Seedling morphology

Habit sketches of a seedling of each of the biennial species included in this study are presented in Figure 5.1. Seedlings of *Verbascum blattaria*, *Verbascum thapsus*, *Oenothera biennis*, *Echium vulgare*, *Cirsium vulgare*, *Onopordum acanthium*, *Lactuca scariola*, and *Dipsacus sylvestris* had leaves which were oriented horizontally to the soil (Figure 5.1 a-c). Seedlings of *Alliaria petiolata*, *Melilotus alba*, *Melilotus officinalis*, *Daucus carota*, *Tragopogon dubius*, *Arctium minus*, and *Tragopogon pratensis* had leaves which were oriented perpendicular to the soil (Figure 5.1 c-e).

Figure 5.1. Habit sketches of seedlings of 15 biennial species which occur in the Marshall pit (x1).

Right: *Verbascum blattaria*

Center: *Verbascum thapsus*

Left: *Oenothera biennis*

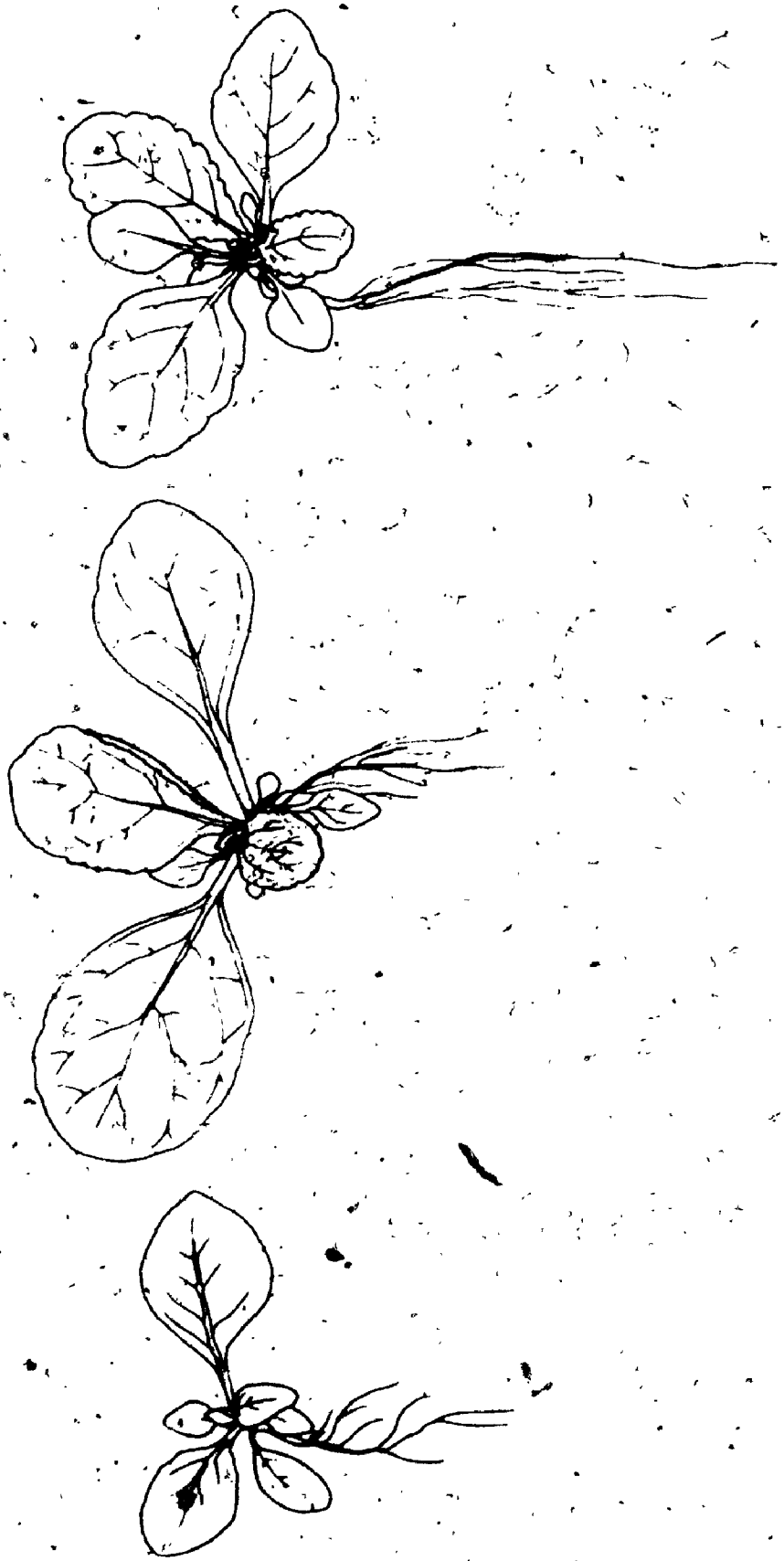


Figure 5.1 Continued

Right; *Echium vulgare*

Center: *Cirsium vulgare*

Left: *Onopordum acanthium*

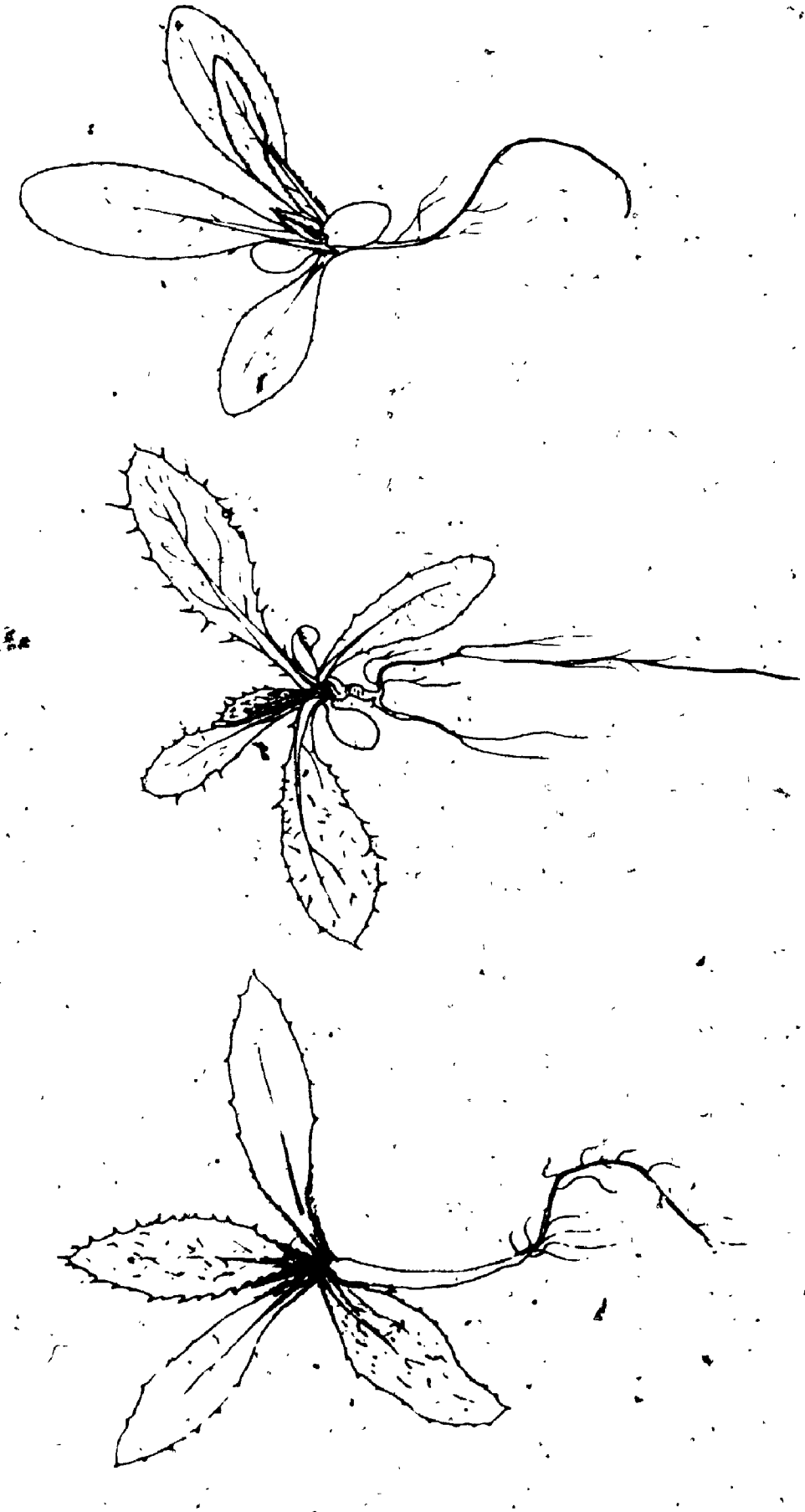


Figure 5.1. Continued

Right: *Alliaria petiolata*

Center: *Lactuca scariola*

Left: *Dipsacus sylvestris*

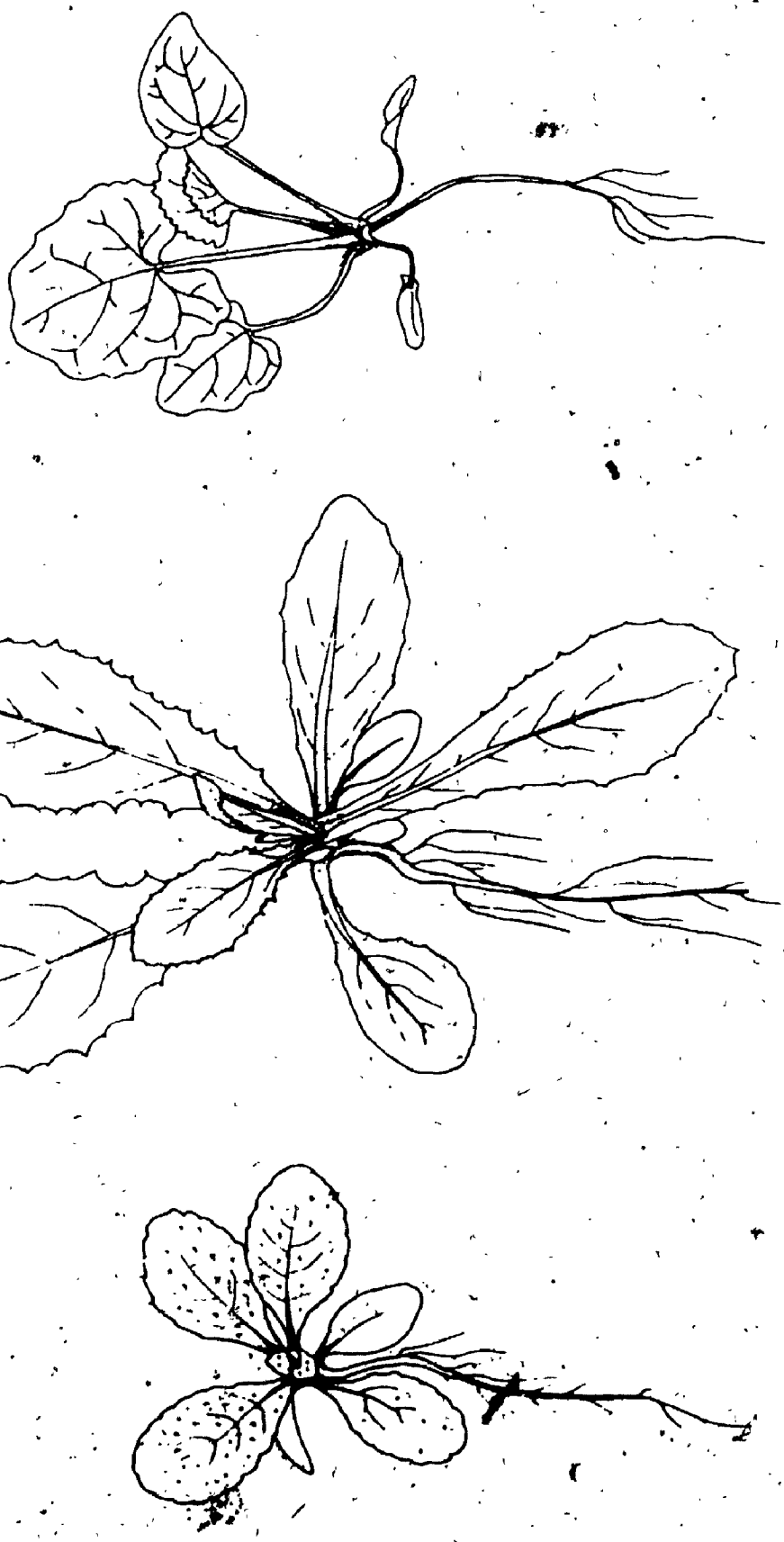


Figure 5.1. Continued

Right: *Melilotus alba*

Center: *Melilotus officinalis*

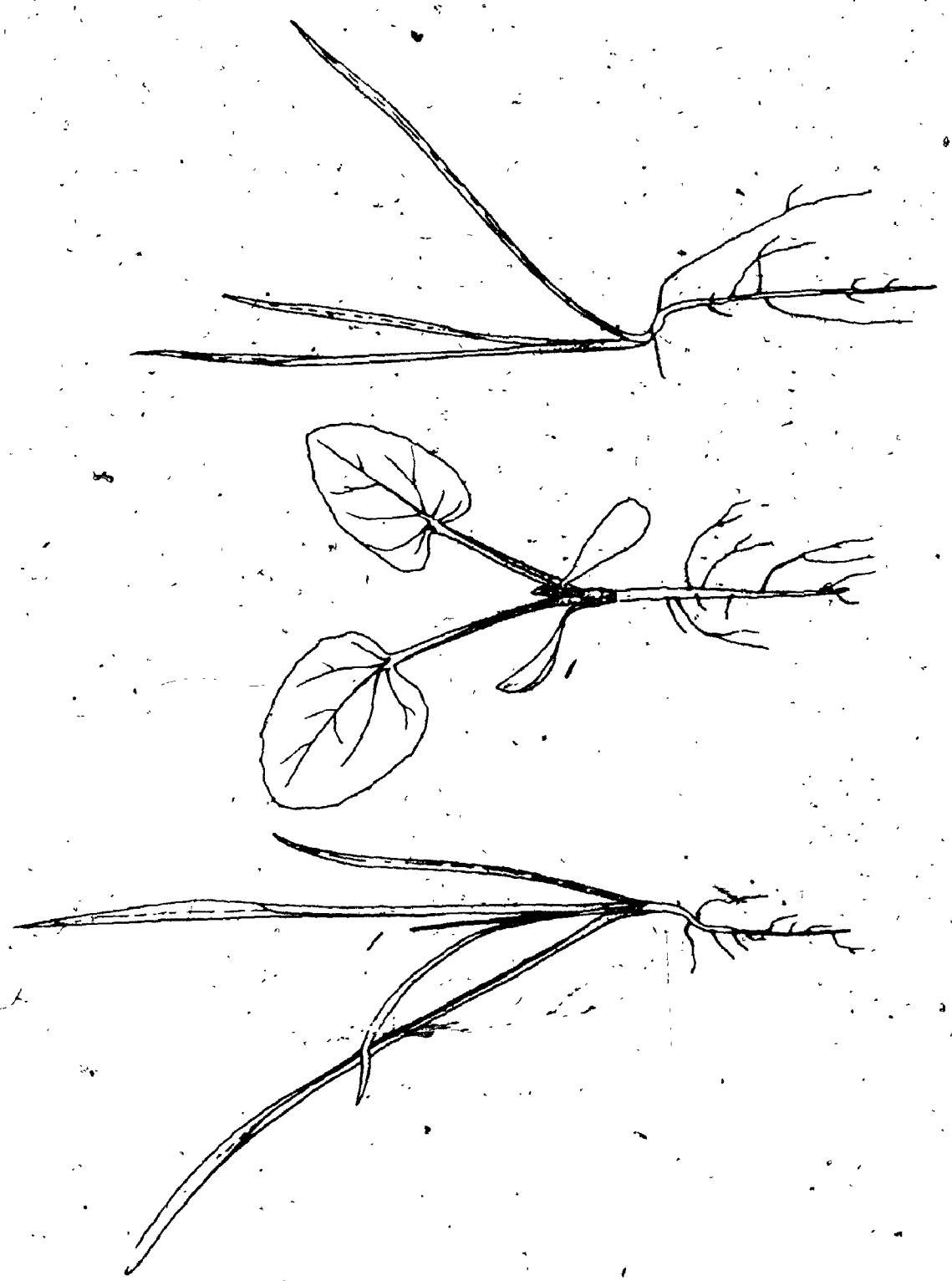
Left: *Daucus carota*

Figure 5.1. Concluded

Right: *Tragopogon dubius*

Center: *Arctium minus*

Left: *Tragopogon pratensis*



B. Emergence

Statistically significant ($P<0.05$) differences in mean seedling emergence existed between taxa within both the sparse and dense cover classes. Mean seedling emergence for each taxon in both sown and unsown plots in both sparse and dense cover classes is presented and compared both between taxa within a cover class and within each taxon between cover classes in Table 5.1. For every taxon which had seedling emergence, values for the number of seeds which produced seedlings were highly variable between plots within each cover class. Seedlings from only 2 species, *Daucus carota* and *Oenothera biennis* emerged in the unsown plots in either cover class. Among the sown plots significantly ($P<0.05$) more seedlings of *Dipsacus sylvestris*, *Lactuca scariola*, and *Verbascum* spp. emerged in sparse than in dense cover. Within both dense and sparse cover the emergence of *Daucus carota* was significantly ($P<0.05$) greater than that of any other taxon. No statistical differences in mean seedling emergence existed among other taxa within either cover class.

Comparisons of expected seedling emergence with actual mean seedling emergence are presented for each cover class in the sown plots in Table 5.2.. In plots in sparse cover 7 taxa had actual emergence which was significantly ($P<0.05$) less than expected and *Alliaria petiolata* failed to emerge. In plots in dense cover 8 taxa had actual emergence which was significantly ($P<0.05$) less than expected and *Alliaria petiolata* failed to emerge.

	Sown			Unsown	
Species	Sparse		Dense	Sparse	Dense
Alliaria petiolata	0.0	ns	0.0	---	---
Arctium minus	132.0±60.8	ns	79.0± 47.6	---	---
Cirsium vulgare	50.0±13.0	ns	64.7± 12.9	---	---
Daucus carota	394.0±111.4	ns	470.0±291.1	331.0±49.5	110.5±105.4
Dipsacus sylvestris	139.7±18.0	**	64.0± 10.5	---	---
Echium vulgare	48.3±29.6	ns	21.7± 12.7	---	---
Lactuca scariola	136.0±16.1	*	54.3± 36.0	---	---
Melilotus spp.	114.0±25.5	ns	41.3± 42.2	---	---
Oenothera biennis	131.7±145.2	ns	35.7±14.6	14.5±12.0	3.0±1.4
Onopordum acanthium	5.7±2.1	ns	4.3±4.2	---	---
Tragopogon spp.	11.0±3.5	ns	74.7±47.5	---	---
Verbascum spp.	126.3±49.2	*	28.0± 20.8	---	---

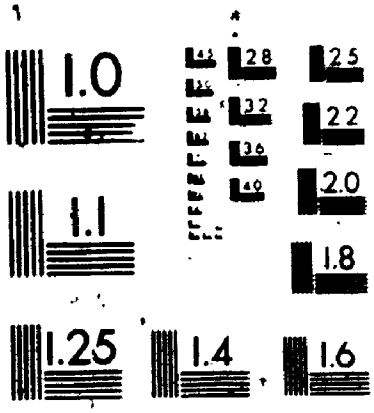
** = significant difference at P<0.01
* = significant difference at P<0.05
ns = not significant at P<0.05.

Table 5.1. Comparison of the mean numbers (± S.D.) of seedlings of biennial taxa which emerged within both sparsely and densely vegetated sown plots, and the mean numbers (± S.D.) of seedlings of each taxon which emerged in unsown plots.

	Cover Class				
	Sparse				Dense
Species	Actual Emergence		Expected Emergence		Actual Emergence
Alliaria petiolata	0.0±0.0	ns	0	ns	0.0±0.0
Arctium minus	132.0±60.8	ns	299	ns	79.0± 47.6
Cirsium vulgare	58.0±13.0	**	291	**	64.7± 12.9
Daucus carota	394.0±111.4	ns	295	ns	470.0±291.1
Dipsacus sylvestris	139.7±18.0	*	300	**	64.0± 10.5
Echium vulgare	48.3±23.6	ns	63	ns	21.7± 12.7
Lactuca scariola	136.0±16.1	*	300	*	54.3± 36.0
Melilotus spp.	114.0±25.5	*	386	*	41.3± 42.2
Oenothera biennis	131.7±145.2	ns	297	**	35.7±14.6
Onopordum acanthium	5.7±2.1	*	26	*	4.3±4.2
Tragopogon spp.	11.0±3.5	**	800	**	74.7±47.5
Verbascum spp.	126.3±49.2	*	599	**	28.0± 20.8

*=significant difference at P<0.05.
**=significant difference at P<0.01.
ns = no significant difference at P<0.05

Table 5.2. Comparison of expected with observed emergence of seedlings for each of 12 biennial taxa in sown plots in both sparsely and densely vegetated plots in the Marshall pit.



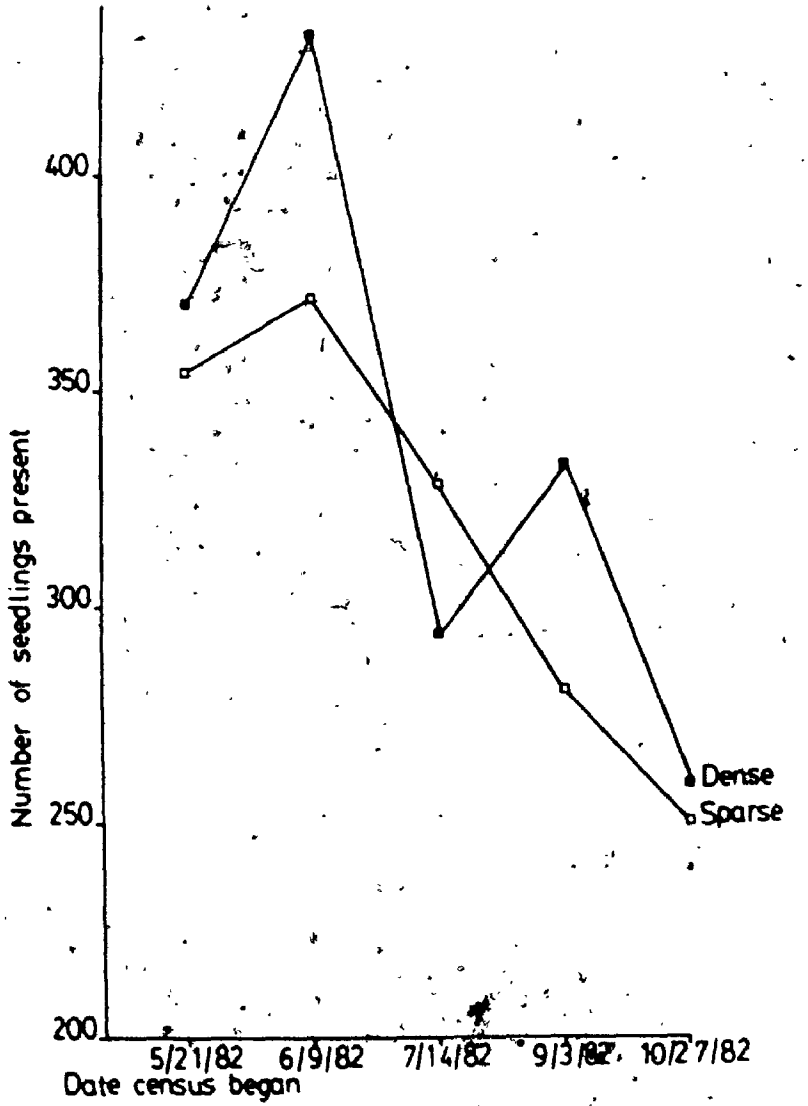
C. Changes in seedling numbers over time

The numbers of emerged seedlings of each taxon present on each of five sampling dates are presented in Figures 5.2 through 5.7. No seedlings of *Alliaria petiolata* emerged, so no figure is presented for this species. On each figure the numbers of seedlings on sparsely and densely vegetated plots are presented on the same set of axes. Seedling mortality in every taxon was apparently the result of desiccation.

The patterns of changes in seedling numbers can be roughly divided into three groups. *Arctium minus* (Figure 5.2), *Dipsacus sylvestris* and *Lactuca scariola* (Figure 5.3), *Echium vulgare* (Figure 5.4), *Oenothera biennis* (Figure 5.5), and *Verbascum* spp. (Figure 5.6) all had greater emergence under sparse cover than under dense cover, suffered continuous mortality once peak seedling numbers had been attained, and incurred the greatest portion of this mortality between the June and September census dates. Of the taxa in this group, all except *Verbascum* spp. attained peak seedling numbers in the June rather than the May census period in the dense plots. *Arctium minus*, *Lactuca scariola*, and *Verbascum* spp. had >60% mortality in plots in both sparse and dense cover. *Dipsacus sylvestris* and *Echium vulgare* had >60% mortality in sparse cover but <50% mortality in the dense cover. *Oenothera biennis* had <50% mortality in plots in sparse cover and <40% mortality in plots in the dense cover.

Onopordum acanthium (Figure 5.4) and *Cirsium vulgare* (Figure 5.5) both had greater emergence in the plots in dense cover than in those in sparse cover, both suffered continuous mortality once peak emergence had been

Figure 5.2. Numbers of seedlings of *Arctium minus* (right) and *Daucus carpta* (left) which were present in the Marshall pit in plots within each of 2 cover classes during 5 census periods.


400
350
300
250
200
Number of seedlings present
Dense
Sparse
5/21/82
6/9/82
7/14/82
9/3/82
10/27/82
Date census began

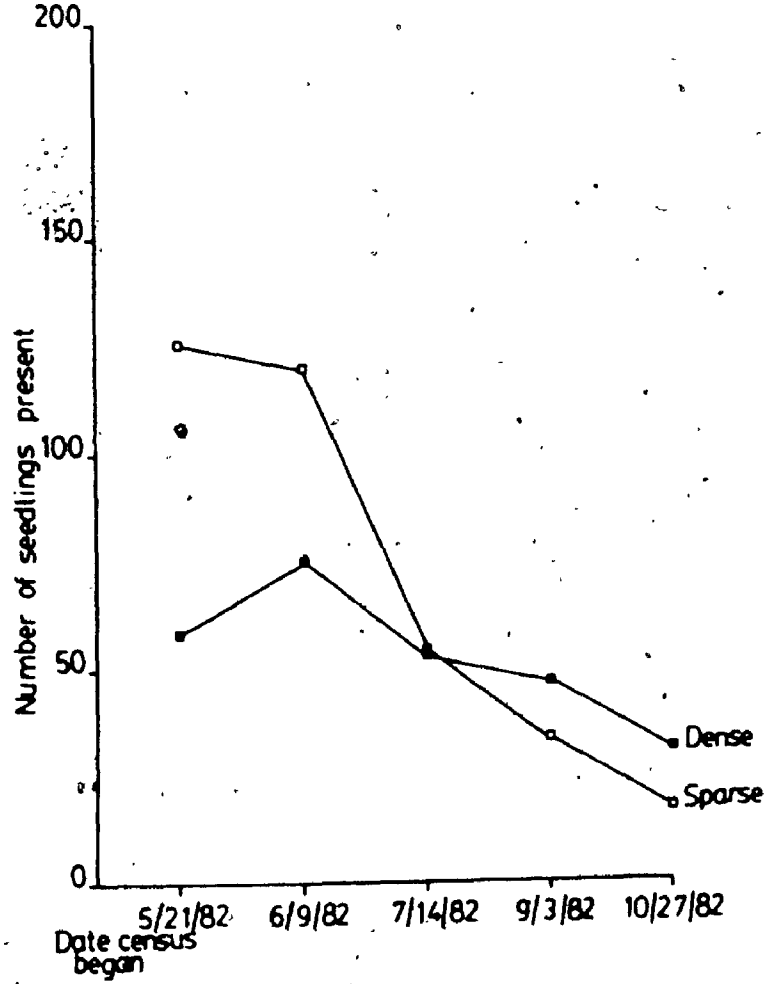
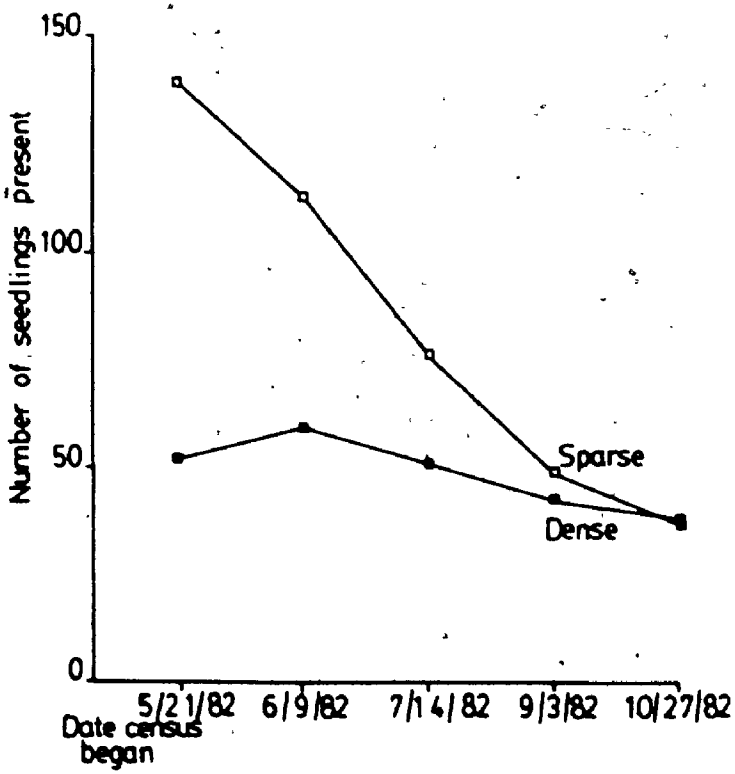

200
150
100
50
0
Number of seedlings present
Dense
Sparse
5/21/82
6/9/82
7/14/82
9/3/82
10/27/82
Date census began

Figure 5.3. Numbers of seedlings of *Lactuca scariola* (right) and *Dipsacus sylvestris* (left) which were present in the Marshall pit in plots within each of 2 cover classes during 5 sampling periods.


150
100
50
0
Number of seedlings present
Sparse
Dense
5/21/82
6/9/82
7/14/82
9/3/82
10/27/82
Date census began

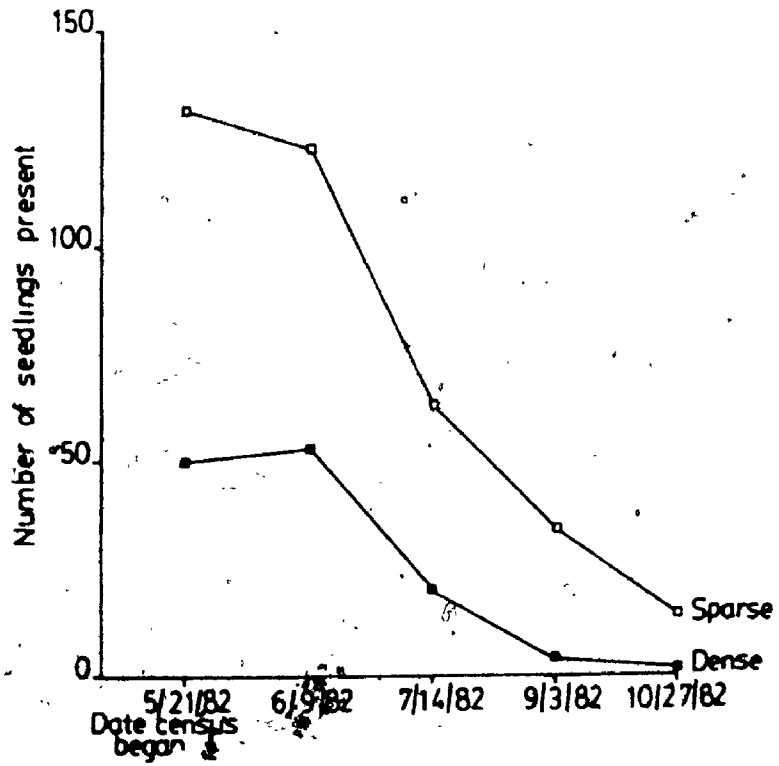
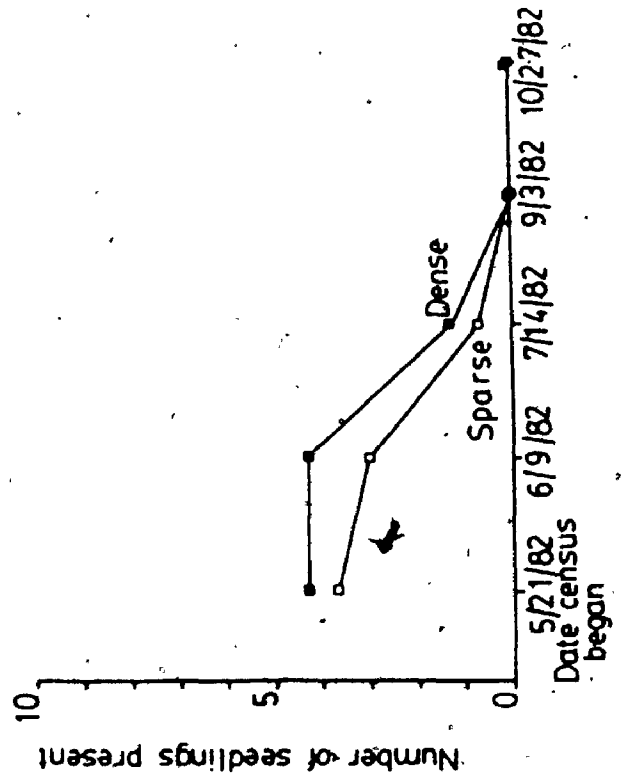

150
100
50
0
Number of seedlings present
Sparse
Dense
5/21/82
6/9/82
7/14/82
9/3/82
10/27/82
Date census began

Figure 5.4. Numbers of seedlings of *Onopordum acanthium* (right) and *Echium vulgare* (left) which were present in the Marshall pit in plots within each of 2 cover classes on 5 sampling dates.


Number of seedlings present
10
5
0
Dense
Sparse
5/21/82
6/9/82
7/14/82
9/3/82
10/27/82
Date census began

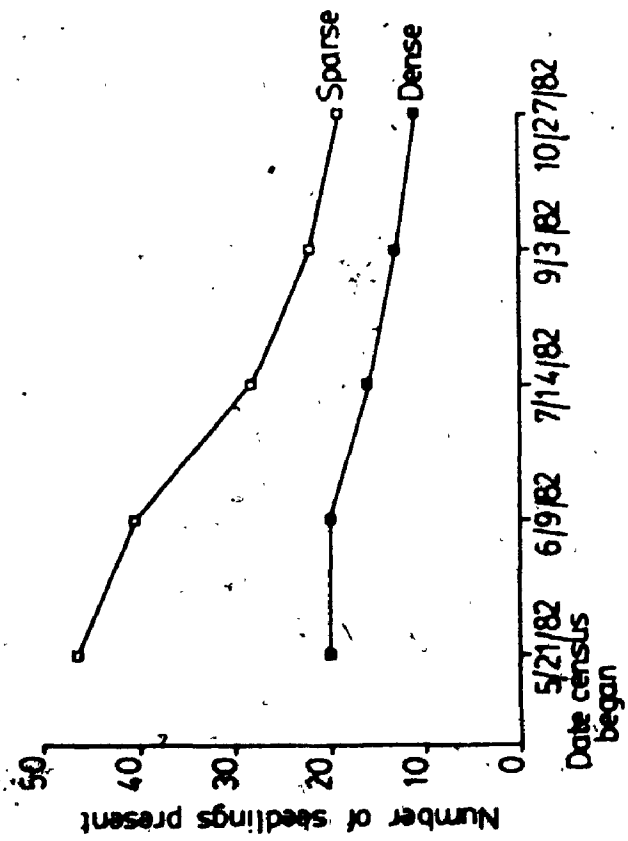
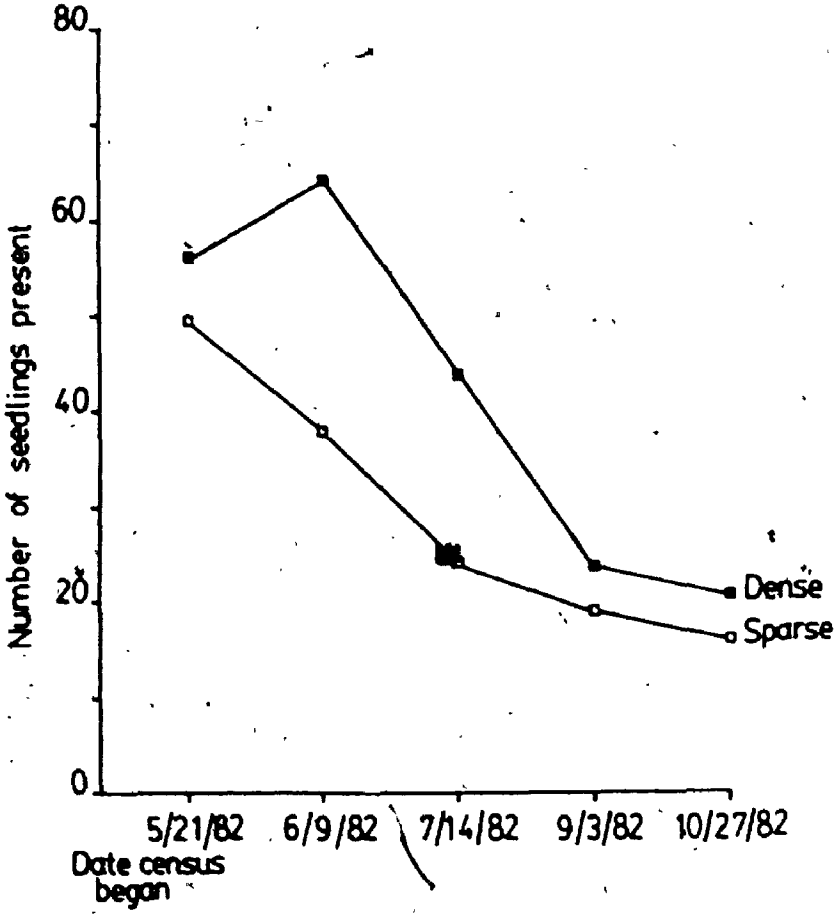

Number of seedlings present
50
40
30
20
10
0
Sparse
Dense
5/21/82
6/9/82
7/14/82
9/3/82
10/27/82
Date census began

Figure 5.5. Numbers of seedlings of *Oenothera biennis* (right) and *Cirsium vulgare* (left) which were present in the Marshall pit in plots within each of 2 cover classes during 5 census periods.


80
60
40
20
0
Number of seedlings present
Dense
Sparse
5/21/82
6/9/82
7/14/82
9/3/82
10/27/82
Date census began

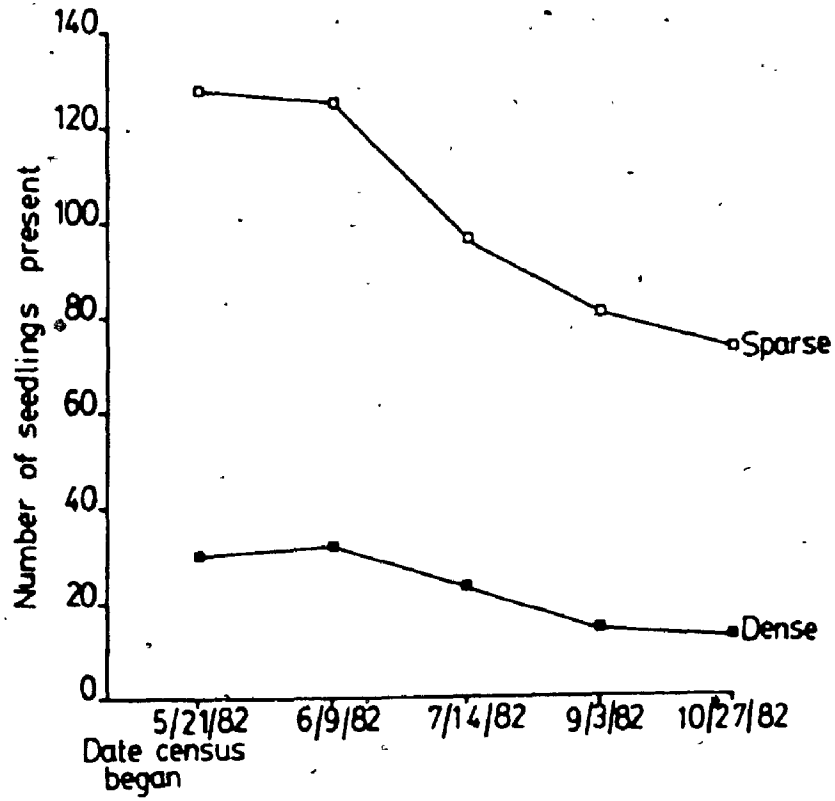
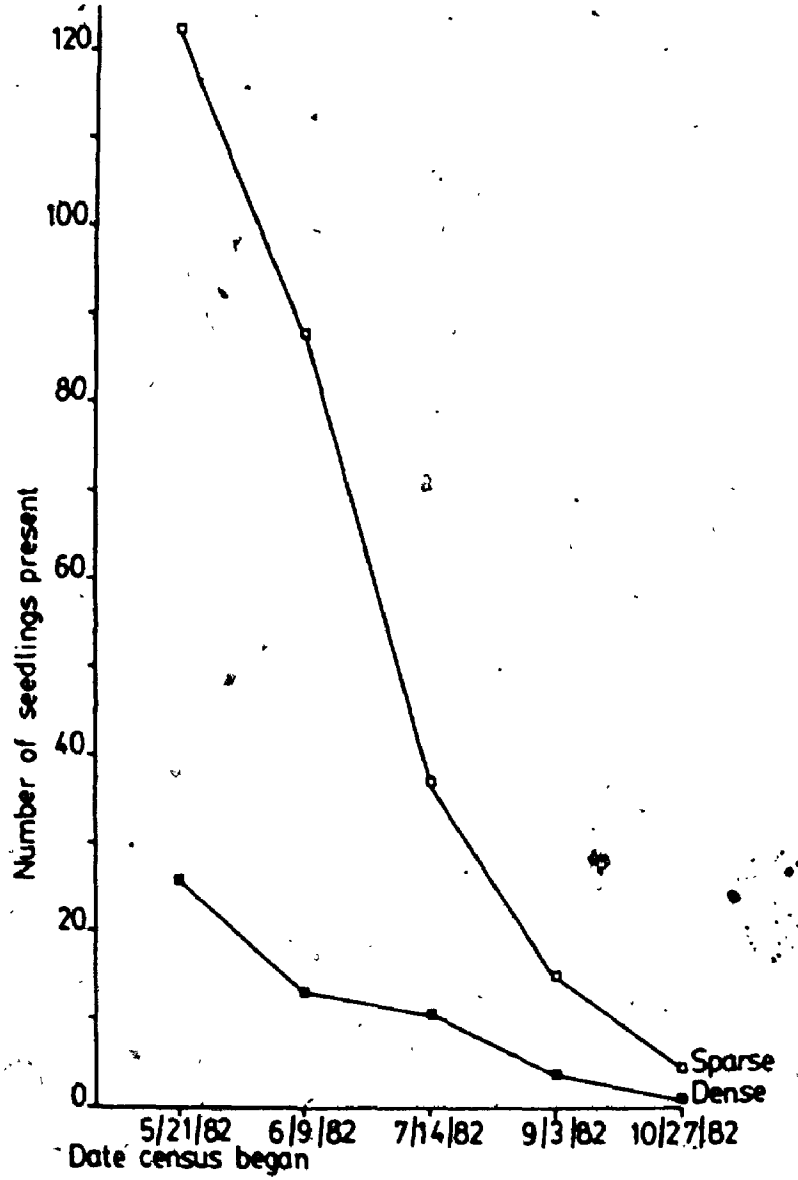

140
120
100
80
60
40
20
0
Number of seedlings present
Sparse
Dense
5/21/82
6/9/82
7/14/82
9/3/82
10/27/82
Date census began

Figure 5.6. Numbers of seedlings of *Melilotus* spp. (right) and *Verbascum* spp. (left) which were present in the Marshall pit in plots within each of 2 cover classes during 5 census periods.


120
100
80
60
40
20
0
Number of seedlings present
Sparse
Dense
5/21/82
6/9/82
7/14/82
9/3/82
10/27/82
Date census began

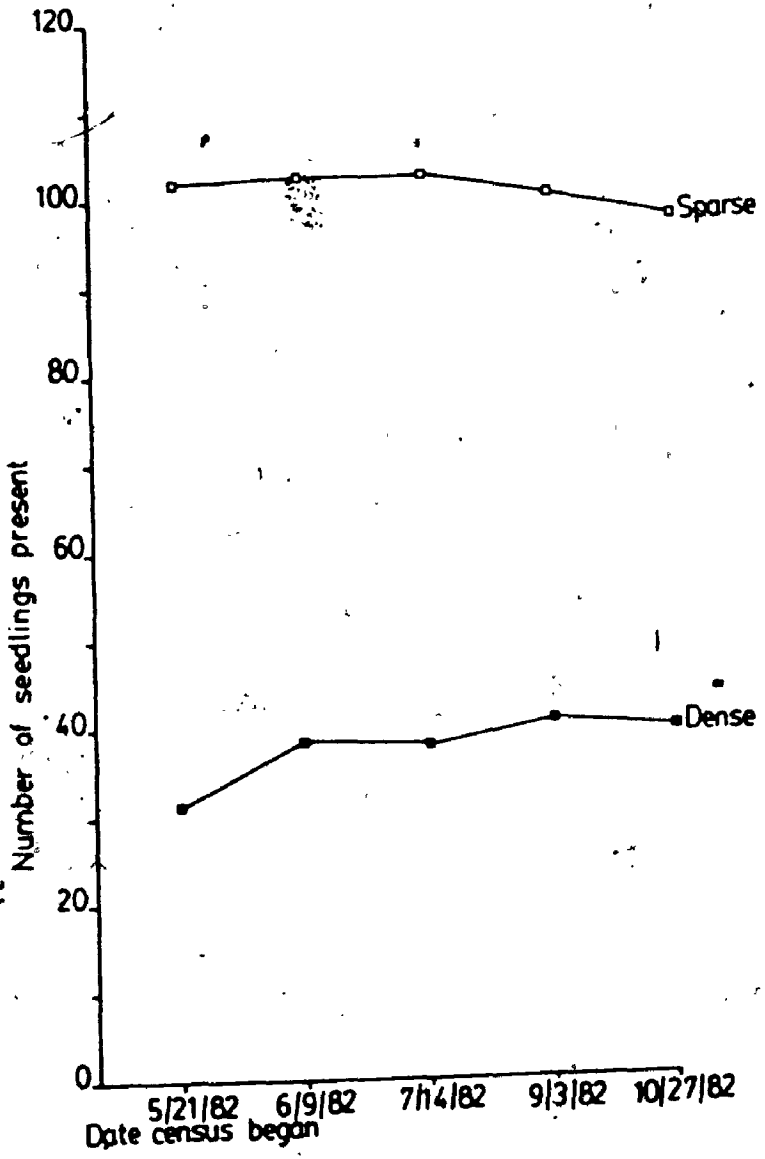
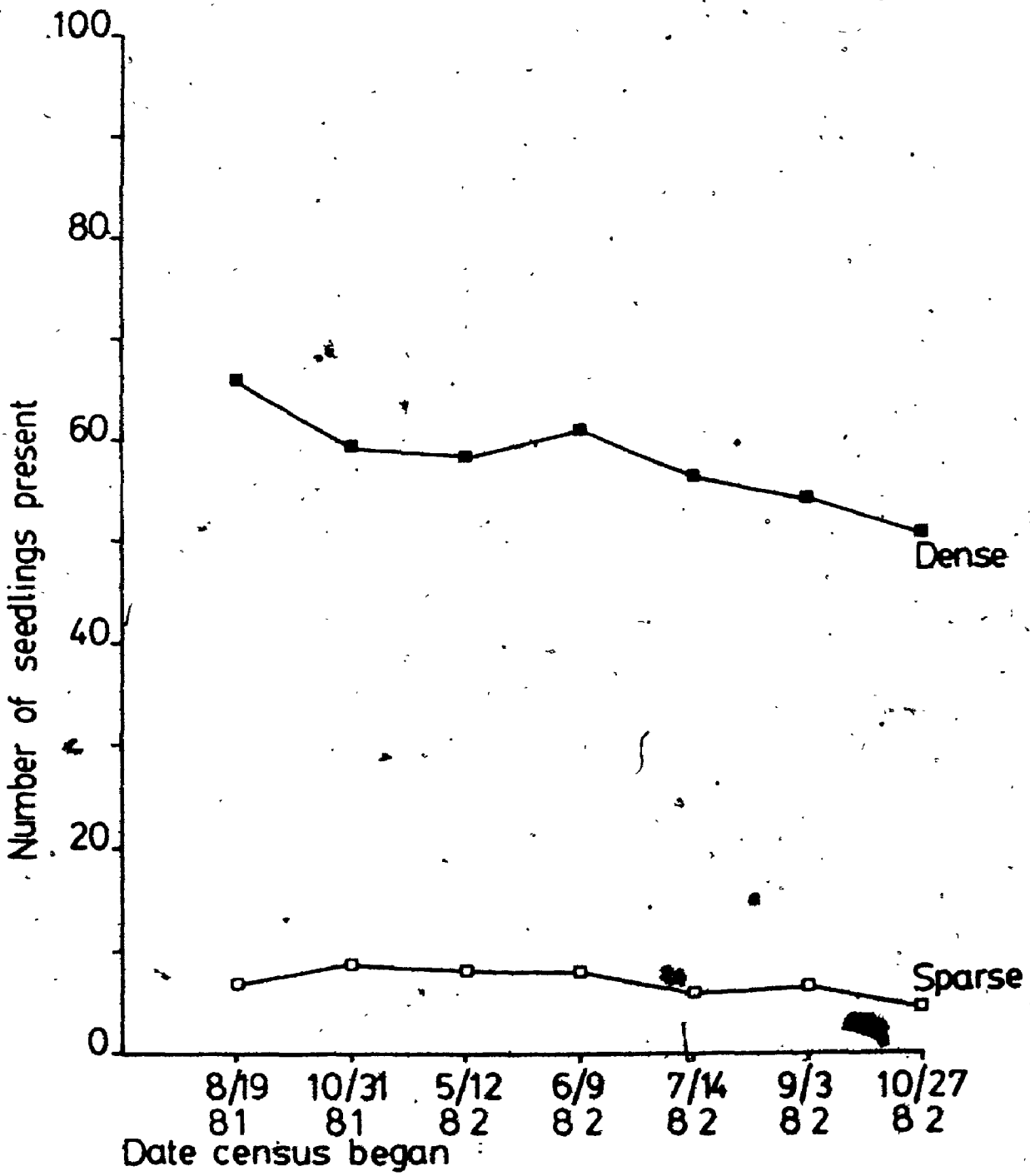

120
100
80
60
40
20
0
Number of seedlings present
Sparse
Dense
5/21/82
6/9/82
7/14/82
9/3/82
10/27/82
Date census began

Figure 5.7. Numbers of seedlings of *Tragopogon* spp. which were present in the Marshall pit in plots within each of 2 cover classes during 7 census periods.


100
80
60
40
20
0
Number of seedlings present
Dense
Sparse
8/19 81
10/31 81
5/12 82
6/9 82
7/14 82
9/3 82
10/27 82
Date census began

attained, and the greatest portion of this mortality was incurred between the June and September census dates. Fewer than 5 individuals of *Onopordum acanthium* emerged in plots in either cover class and no individuals survived the growing season. In plots in dense cover, *Cirsium vulgare* attained peak seedling numbers in the June rather than the May census period. *Cirsium vulgare* had >60% mortality in plots in both sparse and dense cover classes.

The remaining taxa, *Daucus carota* (Figure 5.2), *Melilotus* spp. (Figure 5.6), and *Tragopogon* spp. (Figure 5.7), had at least one pulse of seedling emergence subsequent to their initial emergence. For *Daucus carota* in plots in dense cover, peak numbers of seedlings occurred at the June census. These peak numbers were followed immediately by 32% mortality. A second pulse of emergence occurred before the September census and this pulse was followed by 22% mortality. *Daucus carota* in the sparse plots attained maximum seedling numbers in the June census and subsequent mortality was continuous until the end of the growing season. Fewer than 10 seedlings of *Tragopogon* spp. emerged in the sparse plots and these suffered very little mortality. Many more seedlings of *Tragopogon* spp. were present in the dense plots. A few of these seedlings died during the fall of their emergence, but a second pulse of emergence occurred before the June census. Mortality was continuous following the second pulse of germination. Many more seedlings of *Melilotus* spp. emerged in the sparse plots than in the dense plots. The numbers of seedlings of these taxa in plots in both cover classes hardly changed between census periods. In the dense plots there was a very slight decline in seedling numbers between the June and July censuses, but there was a small pulse of emergence which occurred before

the September census. Very little mortality occurred subsequent to the September census.

D. Seedling establishment

Statistically significant ($P<0.05$) differences in mean percent seedling establishment existed between species within both the sparse and dense cover classes. Mean percent seedling establishment for all taxa in both sparse and dense cover classes is presented in Table 5.3. In both the sparse and dense plots 8 taxa, *Arctium minus*, *Cirsium vulgare*, *Daucus carota*, *Dipsacus sylvestris*, *Echium vulgare*, *Melilotus* spp., *Oenothera biennis*, and *Tragopogon* spp., had a mean percent seedling establishment which was significantly ($P<0.05$) greater than 0. Neither *Alliaria petiolata* nor *Onopordum acanthium* had any seedlings establish in plots in either sparse or dense cover. Comparisons of the mean percent establishment between plots in sparse cover and those in dense cover revealed that for no species was there a statistically significant difference at the 0.05 percent level in mean percent seedling establishment between plots.

5.4 Discussion

A. Seedling morphology

The seedlings of the biennial species included in this study were quite variable in their morphology (Figure 5.1). Fenner (1985) noted that there is little information available concerning the adaptations of seedlings to the environment. Gross (1984) however, investigated the establishment of

Species	Cover Class: Sparse	Dense
Alliaria petiolata	0g	0d
Arctium minus	14.3 ± 5.5def	34.3 ± 27.4bc
Cirsium vulgare	32.2 ± 11.9cde	36.3 ± 35.2bc
Daucus carota	63.7 ± 10.6ab	65.0 ± 25.5ab
Dipsacus sylvestris	27.3 ± 10.7cde	56.7 ± 26.3ab
Echium vulgare	34.7 ± 13.2bcde	56.7 ± 16.1ab
Lactuca scariola	10.0 ± 5.6efg	9.7 ± 16.7cd
Melilotus spp.	82.7 ± 14.0a	91.7 ± 7.6a
Oenothera biennis	56.3 ± 10.1abc	39.3 ± 14.0bc
Onopordum acanthium	0g	0d
Tragopogon spp.	39.7 ± 15.9bcd	63.7 ± 12.5ab
Verbascum spp.	3.7 ± 2.1fg	6.7 ± 9.9cd

Table 5.3. Mean percent (± S.D.) of seedlings of 12 biennial taxa which survived to establish within both sparsely and densely vegetated plots in the study area in the Marshall pit. Entries within a column followed by the same letter are not significantly different ($P<0.05$).

seedlings of 6 biennial species in a variety of cover types in a greenhouse. She selected *Arctium minus*, *Daucus carota*, *Dipsacus sylvestris*, *Oenothera biennis*, *Tragopogon dubius*, and *Verbascum thapsus* for study because of their widely varying seedling morphologies. Gross (1984) found that for each of these species seed size, rather than growth form of the seedling, was the factor most responsible for successful establishment. It is possible, nonetheless, that the differing seedling morphologies of my biennial species might be of significance to their emergence and establishment in the field. This aspect of their respective life histories merits further investigation.

B. Emergence

A freshly matured seed faces an uncertain environment. It must avoid predation before its dispersal, and once dispersed, must lodge in a microsite where conditions are either favorable for its immediate germination, or have the potential to become favorable for breaking its dormancy. A seed dispersed into a habitat where disturbance is unpredictable in time must also avoid both post-dispersal predation and becoming entombed in a seed bank in a state of enforced dormancy where it may die before it can germinate (4.4 C.). Many seeds do not avoid such hazards and consequently, only a fraction of the seeds produced by a plant emerge as seedlings. Hickman (1979) has stated that 95% of plant mortality occurs at the seed stage before the seedling has emerged.

Each plant species has a unique dormancy behavior and a specific set of germination requirements which presumably have been adopted to maximize the probability that a seedling will emerge into a microsite where

there is a high probability of successful establishment (Fenner 1985). If seeds from a number of species are sown into a given habitat, because of the array of unique microsites present in that habitat, there will be differences between species in the numbers of seedlings which emerge.

In my study variation occurred between species in the mean number of seedlings which emerged within both the sparsely and densely vegetated plots. The relatively large numbers of *Daucus carota* seedlings which emerged in each cover class, however, overshadowed the differences in emergence which existed between and within the other taxa (Table 5.1). As evidenced by their emergence in the unsown plots, however, the numerous *Daucus carota* seedlings were probably the result of an unknown contribution from a large persistent seed bank rather than from nearly complete emergence of sown seeds (Table 5.1). The only other species which had seedling emergence contributed from a pre-existing persistent seed bank, *Oenothera biennis*, had relatively small numbers of seedlings emerge in the control plots compared with those which emerged in the sown plots. Thus, emergence in the sown plots by seedlings of this species originating from seeds in a pre-existing seed bank was probably negligible (Table 5.1).

The conditions which prevail in closed vegetation are such that it is very difficult for a newly emerged seedling to capture sufficient resources to develop in competition with established plants (Grubb 1977, Harper 1977, Cook 1979, Silvertown 1981, Fenner 1985). Many studies have shown that regeneration from seed in closed vegetation is dependent on the presence of gaps in the foliar canopy (Cavers and Harper 1967a, Holt 1972, Platt 1975, Grubb 1976, Fenner 1978, Thompson and Grime 1979, Gross and Werner

1982, Gross and Werner 1983, Hartgerink and Bazzaz 1984, Reinartz 1984b). Many species, including a number of the biennials in this study (4.4 B.), have mechanisms which prevent seed germination under conditions which have a high probability of being unfavorable for subsequent establishment (Fenner 1985). Consequently, it was expected that fewer biennial seedlings would emerge in the densely vegetated plots than in the sparsely vegetated plots. In only three taxa, *Cirsium vulgare*, *Daucus carota*, and *Tragopogon* spp., was there a tendency for more seedlings to emerge in the dense sites, but in each case the tendency was statistically nonsignificant ($P>0.05$) (Table 5.1). In three cases when statistically fewer seedlings did occur in the dense sites, lowered emergence was undoubtedly the direct result of inhibition of germination by factors asspciated with the dense vegetation. In two of these taxa, *Lactuca scariola* and *Verbascum* spp., germination is strongly inhibited by light filtered through a leaf canopy (Baskin and Baskin 1981, Gross 1985, Marks and Prince 1982). The third, *Dipsacus sylvestris*, was shown by Werner (1975b) to have its germination strongly inhibited by litter of *Agropyron repens* litter. The germination of one other species, *Oenothera biennis*, is strongly inhibited by light filtered through a leaf canopy (Gross 1985), but its emergence was so variable in the sparse plots (Table 5.1) that no statistical difference between cover types was detected.

There are reports in the literature of the percentage emergence in the field from seeds of most of the biennial species in this study. Cavers et al. (1979) reported no emergence of *Alliaria petiolata* in the year following sowing. Roberts and Chancellor (1979) obtained from 0.4 to 35.0% emergence for *Cirsium vulgare* in the autumn of sowing and from 35.0 to 74.4% emergence

in the following year. Gross and Werner (1983) noted 2.6% emergence of *Arctium minus* when seeds were sown into vegetation and 8.3% emergence when they were sown into plots where the vegetation had been clipped. Verkaar and Schenkeveld (1984b) reported 31.5% emergence for *Daucus carota* in a dune system and Holt (1972) had 42.0% emergence for this species in an old field. Gross and Werner (1982) obtained only 11.0% emergence for *Daucus carota* in a one year old field, 2.3% emergence in a five year old field, and 13.0% emergence in a fifteen year old field. Werner (1975a) reported 0.8% emergence for *Dipsacus sylvestris* seeds sown into *Agropyron repens* litter and 32.0% emergence after the litter had been removed. In a later study Werner (1977) reported 20.0% emergence for the same biennial species when seeds were sown into standing vegetation. Klemow and Raynal (1985) obtained 8.0 to 36.0% emergence for *Echium vulgare* in an abandoned limestone quarry. Marks and Prince (1981) found that emergence of *Lactuca scariola* was never more than 5.0% of the total seed bank. In an abandoned limestone quarry Klemow and Raynal (1981) reported 25.2% emergence for *Melilotus alba* on sparsely vegetated sites and from 11.3 to 66.7% emergence in densely vegetated sites. Gross and Werner (1982) recorded 0.06% emergence for *Oenothera biennis* in a one year old field, 0.01% emergence in a five year old field, and 0.002% in a fifteen year old field. Roberts and Chancellor (1979) reported from 0.7 to 10.8% emergence for *Onopordum acanthium* in the fall of sowing and from 7.1 to 27.3% in the following year. Gross and Werner (1982) obtained 31.0% emergence for *Tragopogon dubius* in a one year old field and 35.0% emergence in both five and fifteen year old fields. Gross and Werner (1982) reported 0.83% emergence for *Verbascum thapsus* in a one year old field, 0.25% emergence in a five year old field, and 0.11%

emergence in a fifteen year old field.

If the germination behavior of freshly matured seeds of the 15 biennials is examined in a controlled environment however, there are statistically significant differences ($P<0.05$) between the expected values and the numbers of seedlings observed to emerge in the field in each cover class for more than half the species. *Oenothera biennis* emerged in expected numbers in the sparse site, but not in the dense site. The seeds of this species are relatively small and though not innately dormant (4.4 B.), they can readily be induced into a deep dormancy by burial or by exposure to leaf-filtered light (Gross 1985). It is likely that many *Oenothera biennis* seeds falling into the dense site were induced into secondary dormancy and were rapidly incorporated into a persistent seed bank. In both cover classes both *Tragopogon* species had less emergence than predicted due to intense post-dispersal seed predation. Although no attempt was made to quantify the numbers of seeds eaten, in the first census after their sowing, every plot which had seeds of *Tragopogon* spp. sown into it was littered with the husks of seeds which had apparently been shelled by a small rodent, probably a species of *Peromyscus* (4.4 E.). Corroborative evidence of predation is presented by Mittlebach and Gross (1984) who found that seeds of *Tragopogon dubius* were readily eaten in a similar fashion by *Peromyscus maniculatus* in an old field in southern Michigan. Seeds of both *Verbascum* species are very small and even though not innately dormant, can readily be induced into deep secondary dormancy by burial or by exposure to leaf-filtered light (Semenza et al. 1978, Baskin and Baskin 1981, Gross 1985). It is probable that many seeds of these species were induced into secondary

dormancy by the prevailing conditions in the soil where they lodged and became incorporated into the persistent seed bank (4.4 C.). Most seeds of *Onopordum acanthium* are innately dormant (Roberts and Chancellor 1979). This dormancy is based on a water soluble inhibitor which must be leached out before germination can occur (4.4 B.). In a controlled environment, seeds of this species germinate in greater numbers when supplied with high alternating temperatures (4.4 B.). Probably the low emergence of *Onopordum acanthium* is a result of a favorable temperature regime for germination occurring at a time of year when there is insufficient water in the soil either to remove the inhibitor or to allow the seed to imbibe. Seeds of this species, if they are able to escape predation and become buried, probably become incorporated into a persistent seed bank (4.4 C.). In my study both *Melilotus* species were found to produce a relatively small persistent seed bank (4.3 C.). Species of *Melilotus* produce a few seeds which are 'soft' and capable of germination immediately upon maturity (4.4 B.). Most seeds of these species are rapidly incorporated into the soil (4.4 C.). Hamly (1932) found that heating hard seeds of *Melilotus alba* increased the permeability of their strophioles to water and would permit them to germinate. Studies of other hard-seeded legume species have indicated that fluctuating diurnal temperatures of the magnitude encountered by seeds in the soil are undoubtedly sufficient to induce the strophioles of their seeds to become permeable to water and thereby permit their germination (Miles 1974, Grime et al. 1981). Given the extreme diurnal fluctuations in temperature which occur in the Marshall pit, it is likely that many seeds of both *Melilotus* species become permeable and germinate either at too great a depth for successful emergence or in a microsite where a seedling cannot establish,

and so many seedlings die before they emerge. Klemow (personal communication) found that *Melilotus alba* incurred great mortality in an abandoned limestone quarry through seeds which germinated but failed to emerge. The remaining three species, *Dipsacus sylvestris*, *Lactuca scariola* and *Cirsium vulgare*, have little innate seed dormancy and form small persistent seed banks (Werner 1975a, Werner 1975b, Roberts and Chancellor 1979, Marks and Prince 1981, van Breeman and van Leeuwen 1983, de Jong and Klinkhammer 1986). *Dipsacus sylvestris* has been shown to have its germination inhibited for at least one year by *Agropyron repens* litter (Werner 1975b) so perhaps the very low numbers of seedlings of this species which emerged in the dense plots reflected a group of seeds which remained in enforced dormancy. The low numbers of *Dipsacus sylvestris* seedlings which emerged in the sparse plots were probably the result of post-germination, pre-emergence mortality rather than incorporation into the seed bank. Marks and Prince (1981) found that in Britain, seeds of *Lactuca scariola* survive in the soil less than 18 months. Most seeds of this species which overwinter there attempt to germinate in the spring rather than die in place (Marks and Prince 1981). Probably the low numbers of *Lactuca scariola* seedlings which emerged in both cover classes in my study resulted from post-germination, pre-emergence mortality. Van Leeuwen (1981) found that in sand dune areas in the Netherlands the germination of *Cirsium vulgare* seeds was influenced by microbial activity. In nutrient-poor sites this activity inhibited germination. In a dune system in the Netherlands, de Jong and Klinkhammer (1986) found that seed predation was the major reason for scarcity of seedlings of *Cirsium vulgare*. With the exception of the two *Tragopogon* species, where the effects of predation were evident,

I found no remnants of predated seeds in the field. Perhaps the scarcity of seedlings of *Cirsium vulgare* in the Marshall pit was the result of either post-dispersal seed predation or inhibition of germination as a result of microbial activity.

C. Seedling establishment

Once a seedling has emerged it is particularly vulnerable to the detrimental effects of severe environmental conditions and competition from other plants until its root and shoot systems have expanded sufficiently to make it self-supporting (Fenner 1985). Many studies have shown that mortality among post-emergent seedlings is great, often ranging from 75 to 100% (Darwin 1860, Harper 1967, Naylor 1972, Sarukhan and Harper 1973, Sharitz and McCormick 1973, Kawano and Nagai 1975, Werner 1975a, Werner 1975b, Hawthorn and Cavers 1976, Mack 1976, Symonides 1977, King 1977b, Turkington et al. 1978, Cavers et al. 1979, Baskin and Baskin 1979a,b, van der Meijden and van der Waals-Kooi 1979, Cook 1979, Gross 1980, Klemow and Raynal 1981, Silvertown and Dickie 1981, Marks and Prince 1981, Gross and Werner 1982, Verkaar and Schenkeveld 1984a, de Jong and Klinkhammer 1986). Many studies which identify the agent of seedling mortality indicate that desiccation is a major cause of death among young seedlings (King 1977b, Watkinson 1978, Mack 1976, Sharitz and McCormick 1973, Cook 1979). Based on my observations, all of the mortality which occurred among biennial seedlings in my study was the result of desiccation because of the aridity of the substrate in the Marshall pit (2.3 D.). Generally, the most serious obstacle to the establishment of newly emerged seedlings is competition from

neighboring plants (Harper 1977, Fenner 1985). There is evidence however, that in extremely dry environments seedling survival may be enhanced by the ameliorating effect of surrounding vegetation (Harper and Chancellor 1959, Turner et al. 1966, Klemow and Raynal 1981, Klemow and Raynal 1985). Seedlings of 4 of the biennial taxa were detrimentally affected both by the harshness of the environment and by competition from the surrounding vegetation. Three of these, *Lactuca scariola* (Figure 5.3), *Onopordum acanthium* (Figure 5.4), and *Verbascum* spp. (Figure 5.6) had more than 90% mortality in plots in both cover classes, whereas one species, *Cirsium vulgare* (Figure 5.5) had approximately 65% mortality in plots in both cover classes. Seedlings of *Oenothera biennis* (Figure 5.5) were detrimentally affected to a greater degree by competition from the surrounding vegetation. Seedlings of four taxa benefited from the ameliorating effects of surrounding vegetation, having greater mortality in the sparse plots. One, *Arctium minus* (Figure 5.2), had 86% mortality in the sparse plot and 66% mortality in the dense plot, whereas the others, *Dipsacus sylvestris* (Figure 5.3), *Echium vulgare* (Figure 5.4), and *Tragopogon* spp. (Figure 5.7), had ≥60% mortality in the sparse and ≤45% mortality in the dense plots. Two taxa, however, *Daucus carota* (Figure 5.2) and *Melilotus* spp. (Figure 5.6), had relatively little seedling mortality in plots in either cover class; less than 36% for *Daucus carota* and less than 19% for seedlings of *Melilotus* spp.. No statistically significant differences ($P>0.05$) existed in the mean percentage of seedling survival of any species between cover classes.

A few studies have reported the percentage of emerged seedlings of monocarpic perennial species which survive to flower (Baskin and Baskin

1979a; Baskin and Baskin 1979b, Cavers et al. 1979, Marks and Prince 1981). There are also records in the literature of the percent of emerged seedlings of monocarpic perennial species which successfully establish. De Jong and Klinkhammer (1986) reported 23 to 47% establishment of seedlings of *Cirsium vulgare* in a dune system, depending on the year. Verkaar and Schenkeveld (1984b) found that seedling survival of *Daucus carota* in a dune system ranged from 50 to 66%, depending on the year. Holt (1972) obtained 61% establishment of seeds of *Daucus carota* in bare ground and 86% establishment in an *Andropogon* sod. Gross (1980b) recorded 22 ± 3.3% establishment of *Daucus carota* seedlings in a 1 year old field and 2.0 ± 0.4% establishment in a 15 year old field. Werner (1975a) found that the establishment of seedlings of *Dipsacus sylvestris* in a series of old fields ranged from 23.3% to 58.2% depending on the percent ground cover. Klemow and Raynal (1985) reported that the percent establishment of seedlings of *Echium vulgare* in an abandoned limestone quarry ranged from 9 to 31% in sparsely vegetated plots and from 13 to 17% in densely vegetated plots. The percent establishment of seedlings of *Melilotus alba* in an abandoned limestone quarry ranged from 0 to 33% in sparsely vegetated plots and from 3.9 to 32% in the densely vegetated sites, depending on the year (Klemow 1982). Gross (1980a) reported that 54% of emerged seedlings of *Oenothera biennis* established in a 1 year old field. Twenty-four percent of emerged seedlings of *Tragopogon dubius* were reported to establish in a 1 year old field whereas 17% established in a 15 year old field (Gross 1980a). Gross (1980b) found that 5.3% of emerged seedlings of *Verbascum thapsus* established in a 1 year old field and none established in a 15 year old field.

With the exception of the unexpectedly high percent survival of seedlings of *Melilotus* spp., 82.7% in the sparse plots and 91.7% in the dense plots, the percent seedling survival of the remaining species was similar to that reported in the literature. The *Melilotus* seedlings made very little post-emergent growth, yet virtually all withstood the severe drought and intense heat of summer. At the end of the growing season they had generally not developed past the four-leaf stage. Although I made no effort to follow the fate of any seedling in its second season of growth, in light of Klemow's (1982) findings that *Melilotus alba* seedlings incurred 68% to 100% mortality in an abandoned limestone quarry, it would be of interest to see how many of the relatively small seedlings in my study area successfully overwintered and subsequently formed juvenile rosettes.

It is significant that the taxa which had the greatest percent seedling establishment in both the sparse and the dense plots, *Daucus carota* and *Melilotus* spp. (Table 5.3), also were the most numerous biennials in the study area (Table 2.2). Apparently the key to the success of these taxa is a relatively high seed output (Table 3.2) coupled with avoidance of mortality in the early seedling stage. Given the size of their reproductive outputs (Table 2.2), sufficient numbers of seedlings of the remaining species, with the possible exceptions of *Alliaria petiolata* and *Onopordum acanthium* (Table 5.3), survive to ensure their successful regeneration in the study area. Since the seeds of *Alliaria petiolata* are deeply dormant and under certain conditions have been reported to remain dormant in the soil in the London, Ontario area for at least 18 months (4.4 B.), the term of my study was too brief to accurately assess the emergence and mortality of seedlings of this

species. *Onopordum acanthium* also has very dormant seeds (4.4 B.). Perhaps the prevailing environmental conditions during the year of my investigation were not conducive to breaking dormancy in this species. It is possible that in a different year, environmental conditions might stimulate the emergence of greater numbers of *Onopordum acanthium* seedlings.

Chapter 6

Emergence and establishment of 15 biennial species across a range of soil textures and gap sizes

6.1 Introduction

The pattern of distribution of plant species within a community at a given time is largely the result of events which took place at the seed and seedling stages of the life cycle of the component species (Harper 1977). Werner (1979) has suggested that from the perspective of the individual plant, the environment consists of a matrix where seeds do not germinate and seedlings do not survive, interspersed with patches where seeds do germinate and seedlings do survive. Such patches represent what Harper (1977) has termed 'safe sites'. These he has defined as locations at the size scale of an individual seed wherein a seed may find the necessary stimuli to break dormancy, the proper conditions for subsequent germination, the resources which are required for germination, and where competitors, pathogens, predators, and toxic substances are absent (Harper 1977). The safe site, as defined, is species-specific and the presence or absence of suitable safe sites can regulate the presence and pattern of distribution of species within a community (Harper 1977, Werner 1979). Species diversity may be maintained within a community if the environment is sufficiently heterogeneous that a large number of diverse safe sites are constantly present (Grubb 1977, Cook 1979, Werner 1979).

The environment which the Marshall pit presents to an individual plant is extremely heterogeneous at the scale of the individual seed or seedling. Within the study area (2.2 D., 2.2 F.) soil surface textures vary from coarse gravel to sand to rudimentary soil, and the vegetation cover ranges from 100% to 15%. Much of the portion of the study area having a high percentage of vegetative cover is pockmarked by open areas (hereafter referred to as gaps) of variable dimensions.

Both soil surface texture and gap size have been shown to influence strongly seed germination and seedling establishment. In nature, seeds are dispersed onto soil surfaces which are heterogeneous at the size scale of the individual seed (Harper et al. 1970). Such heterogeneity produces microsites which have different moisture and aeration conditions (Harper et al. 1965, Sheldon 1974, Pareja and Staniforth 1985, Winn 1985). The size and shape of the dispersed seed then interacts with the microsite to determine the existence of a safe site (Harper et al. 1965, Sheldon 1974). Subtle differences exist between species and their response to microsites such that occupation of different safe sites on a soil surface by different species may permit coexistence of a variety of species (Sheldon 1974, Fenner 1985). In closed vegetation, gaps are important for the establishment of new plants by seed (Cavers and Harper 1967a, Holt 1972, Platt 1975, Grubb 1976, Harper 1977, Grubb 1977, Fenner 1978, Cook 1979, Thompson and Grime 1979, Silvertown 1981, Gross and Werner 1982, Gross and Werner 1983, Hartgerink and Bazazz 1984, Reinartz 1984b, Fenner 1985). Gap size has been shown to have an important effect on germination, seedling growth and survival (Davies and Cantlon 1969, Caruso 1970, Fenner 1978, Ross and Harper 1972, Miles 1974,

Gross 1980, Gross and Werner 1982, Goldberg and Werner 1983). Fenner (1985) suggests that size of the gap is probably the single most important feature because many other characteristics of a gap are area-dependent. Gaps differ in the levels of resources they contain. Consequently, different species are able to exploit different sized gaps (Grubb 1976, Grubb 1977, Gross and Werner 1982). The presence of gaps of different sizes in a community may lead to the continued coexistence of species which are differentially able to exploit them (Grubb 1976, Grubb 1977, Gross and Werner 1982, Fenner 1985).

The environment in the Marshall pit is a heterogenous mosaic at the scale of the size of the individual seed. Consequently, I investigated whether or not the co-existence of 15 biennial species could be explained through differences in their species-specific requirements for germination and/or establishment across a range of either soil surface textures or gap sizes. In this chapter my findings are presented, then discussed with respect to the seed weights, germination behavior, and seedling characteristics of the species involved.

6.2 Materials and Methods

A. Experimental design

Two experiments were carried out simultaneously in 1982-83 to investigate the emergence and establishment of seedlings of 15 biennial species in response to 2 physical factors which were deemed to be important in the field, soil texture and the size of the gap present in the standing vegetation. These experiments were performed at the Experimental Field

Station maintained by the Plant Sciences Department. The field station is located north and east of the intersection of Highway 22 and Highway 4 in north London, Ontario 43°02'N, 81°16'W). The plot where these experiments were carried out is adjacent to the eastern fence of the field station grounds. According to Hawthorn (1973), the soil underlying the study site is a Guelph loam. This is a greyish light-brown loam over a reddish or grey sandy loam which overlays a calcareous till derived from dolomitic limestone and shale (Hawthorn 1973). It is a fairly deep and freely drained loam with a pH of 6.8 to 7.0 (Hawthorn 1973).

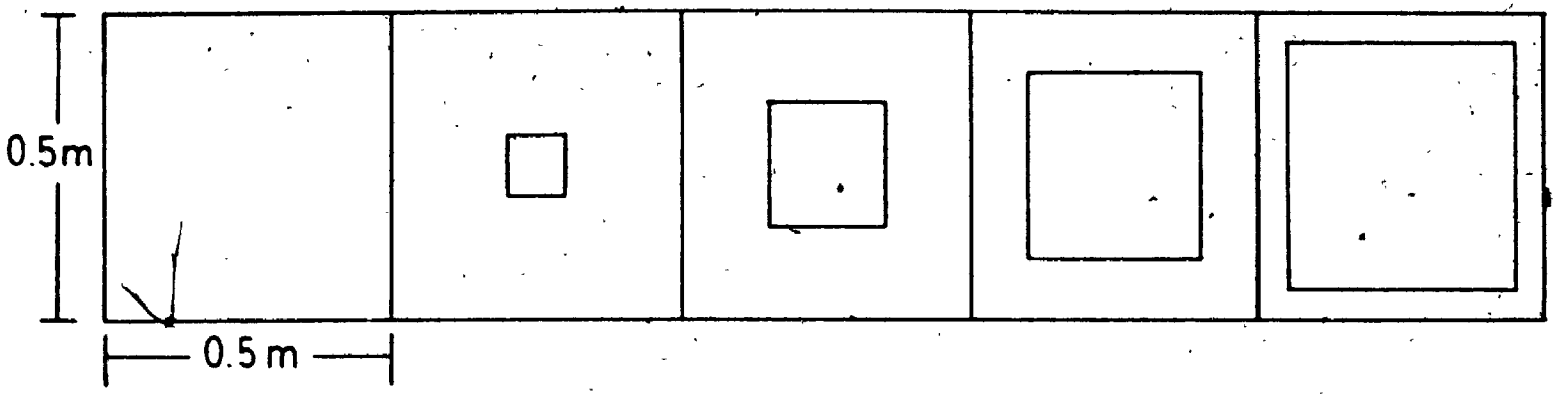
The experimental design is presented in Figure 6.1. Each experiment was based on gradient boxes. A gradient box consisted of 5 incremental treatment levels (henceforth called treatments) of the factor being investigated. In each of the 2 experiments, a gradient box was replicated 4 times.

B. Site preparation

The plot where the experiments were to be carried out was cleared in the spring of 1982 to remove the standing vegetation. Eight trenches were dug, each 2.5 x 0.5m in area and 0.3m in depth. Soil taken from those trenches which were to contain soil texture treatments was removed from the study area. Soil taken from those trenches which were to contain gap size treatments was pasteurized at 82 C to destroy all seeds and organs of vegetative reproduction which might have been present. Then forms were constructed from 2.0cm thick plywood to fit the above-mentioned trenches and contain the experimental treatments. Each form was open both on the

Figure 6.1. Arrangement of treatments in both the gap size and soil texture experiments. Each treatment was replicated 4 times overall.

TREATMENTS IN GAP SIZE AND SUBSTRATE TEXTURE EXPERIMENT



	S= 25 %	S=50 %	S=75 %	S=100 %
G=100 %	G=75 %	G=50 %	G= 25 %	

S=SAND G=GRAVEL

bottom and on the top. It was divided into 5 compartments by the placement of a partition made of 2.0cm plywood at each 0.5m interval throughout its length. Thus, each form was made up of five 0.5 x 0.5m compartments, each of which contained one experimental treatment.

In both experiments the substrate (soil, sand, gravel, or a sand/gravel mix) filled the form level with its top edge. The sand and gravel used to create the soil texture treatments were purchased in processed form from a commercial gravel pit adjacent to the Marshall pit. The gravel used was three-quarter stone (gravel 2cm in diameter or less). The soil textures created are presented in Figure 6.1. In treatments where sand and gravel were mixed, they were mixed by volume. Pasteurized soil from the study site was returned to the forms which were part of the gap size experiment. Once the soil was in place seeds of *Phleum pratense*, obtained commercially, were sown over each gradient box to produce a uniform lawn. This species was chosen because it was common in the gravel pit and its seeds were readily available. Once a uniform lawn had been established, gaps of a range of sizes (40 x 40cm, 30 x 30cm, 20 x 20cm, and 10 x 10cm) were created (Figure 6.1). In the creation of these gaps individual *Phleum pratense* plants were pulled up by the roots so that at the beginning of the experiment, the gap would also extend into the rhizosphere.

C. Seed input

As seeds of the 15 biennial species became ripe in the field, they were collected, processed, and sown into all experimental treatments in both experiments. For each species bulk samples of fruits were collected in the Marshall and West Missouri gravel pits. Once collected, the fruits were kept in dry paper bags at ambient outdoor temperatures until processing could be completed. The processing of seeds varied depending on the nature of the fruit. For *Daucus carota*, *Echium vulgare*, and *Dipsacus sylvestris*, infructescences were pulled apart by hand to separate diaspores; whereas for *Alliaria petiolata*, *Arctium minus*, *Melilotus alba*, *Melilotus officinalis*, *Oenothera biennis*, *Verbascum blattaria*, and *Verbascum thapsus*, the fruit was mechanically ruptured to separate the diaspores. For each species the resultant material was passed through a nest of soil sieves with graded mesh sizes to remove all particles except those near seed size. The seeds were then separated by means of a seed blower. Diaspores of *Cirsium vulgare*, *Lactuca scariola*, *Tragopogon dubius*, and *Tragopogon pratensis* were collected and the pappus removed by hand. It should be noted that removal of the pappus from the achenes of these species could have an effect on their subsequent emergence and establishment. Sheldon (1974) demonstrated that water uptake by achenes of several species of Compositae was most efficient through the attachment scar and that the pappus played an important role in the orientation of the dispersed achene in relation to the soil surface so that contact between the attachment scar and the water-supplying substrate was maximized. Despite this knowledge, it was decided to remove the pappus from the diaspores of each of these species before

sowing to prevent their being blown out of the treatments after sowing. Once cleaned, seeds were sorted into lots for sowing into experimental treatments. The numbers of seeds in each lot varied from species to species.

A constant number of seeds of each species (but different numbers for different species) was sown into each treatment in both experiments (Table 6.1). The size and proportional composition of this mixture was chosen to reflect the relative contributions of each species to the seed rain in the field. Thus, it was based on both the potential reproductive output of each species as determined in the gravel pit and the relative abundance of each species in the study area. Table 4.2 shows that this mixture is not precisely representative of the rain of biennial seeds predicted for the study area. The mixture is a compromise based on a lower limit of 50 seeds per treatment for the two *Tragopogon* species. The sowing density/m^2 of seeds of each species for each treatment in both experiments is presented in Table 6.2. Given the number of seeds of the two *Tragopogon* species which had to be maintained in each treatment, it was felt that if a true proportional representation were given to more fecund species, the density of seeds present in each treatment, particularly the smaller gap sizes, would reach a level where strong interference could occur. The seed densities created using this seed mixture are high in both the 20 x 20cm and the 10 x 10cm gaps. In both cases it exceeds the maximum density of 1.0×10^5 seeds/m^2 which Gross (1980) used for *Verbascum thapsus* in her gap size study in an old field in southern Michigan. In neither case however, does the density created in this experiment greatly exceed that used by Gross. Furthermore, Gross (1980) added all her seeds simultaneously whereas the seed mixture

Species	Date sown	Number of seeds sown per treatment
Daucus carota	9/09/82	500
Melilotus alba	8/28/82	500
Melilotus officinalis	8/06/82	500
Verbascum thapsus	8/24/82	500
Dipsacus sylvestris	10/10/82	400
Onopordum acanthium	8/31/82	400
Oenothera biennis	10/27/82	300
Verbascum blattaria	8/24/82	300
Arctium minus	9/09/82	200
Alliaria petiolata	7/28/82	200
Cirsium vulgare	10/10/82	200
Echium vulgare	8/31/82	200
Lactuca scariola	9/29/82	100
Tragopogon dubius	7/12/82	50
Tragopogon pratensis	7/12/82	50
Total	-------	4400

Table 6.1. Numbers of seeds of each of 15 biennial species which were sown into each treatment of both the soil textures and gap size experiments presented along with the date of their sowing.

Species	All Soil Textures, 40 x 40cm Gap, and No Gap	30 x 30cm Gap	20 x 20cm Gap	10 x 10cm Gap
Daucus carota	3.1×10^3	5.6×10^3	1.2×10^4	5.0×10^4
Melilotus alba	3.1×10^3	5.6×10^3	1.2×10^4	5.0×10^4
Melilotus officinalis	3.1×10^3	5.6×10^3	1.2×10^4	5.0×10^4
Verbascum thapsus	3.1×10^3	5.6×10^3	1.2×10^4	5.0×10^4
Dipsacus sylvestris	2.5×10^3	4.4×10^3	1.0×10^4	4.0×10^4
Onopordum acanthium	2.5×10^3	4.4×10^3	1.0×10^4	4.0×10^4
Oenothera biennis	1.9×10^3	3.3×10^3	7.5×10^3	3.0×10^4
Verbascum blattaria	1.9×10^3	3.3×10^3	7.5×10^3	3.0×10^4
Arctium minus	1.2×10^3	2.2×10^3	5.0×10^3	2.0×10^4
Alliaria petiolata	1.2×10^3	2.2×10^3	5.0×10^3	2.0×10^4
Cirsium vulgare	1.2×10^3	2.2×10^3	5.0×10^3	2.0×10^4
Echium vulgare	1.2×10^3	2.2×10^3	5.0×10^3	2.0×10^4
Lactuca scariola	6.2×10^2	1.1×10^3	2.5×10^3	1.0×10^4
Tragopogon dubius	3.1×10^2	5.6×10^2	1.2×10^3	5.0×10^3
Tragopogon pratensis	3.1×10^2	5.6×10^2	1.2×10^3	5.0×10^3
Total	2.8×10^4	4.8×10^4	1.1×10^5	4.4×10^5

Table 6.2. Density/m^2 at which seeds of each of 15 biennial taxa were sown into each treatment in both the soil texture and gap size experiments.

used in the current study was introduced over a period of 3 months as seeds became ripe in the field (Table 6.1). In this study then, the earlier ripening seeds had opportunity to either germinate or become incorporated into the soil before later ripening seeds were sown, and the density of seeds on the soil at any given time was considerably less than the overall number of seeds added throughout the entire sowing. Although laboratory studies have indicated that when seeds of some species are clumped at high densities, chemical interactions can occur which affect germination, Fenner (1985) suggests that the significance of such effects are yet to be demonstrated in the field. Interference resulting from high seed density at sowing is believed to be negligible in this experiment.

In every treatment in both experiments, seeds of each species were sown by hand. In the soil texture experiment and in the no gap treatment in the gap size experiment, seeds of each species were sown uniformly in the center 40 x 40cm. In the remaining gap size treatments, seeds were sown uniformly throughout the gap. No fertilizer was added to any treatment in either experiment, nor was any water provided other than natural rainfall. Any plant other than one of the 15 biennials of interest which emerged in any treatment in either experiment was removed upon recognition.

D. Data collection

Emerged seedlings were mapped 5 times during the course of the study; twice during the fall of 1982 and three times during the growing season of 1983. Mapping began in the spring of 1983 as soon as the emerging seedlings could be identified to species. Mapping was accomplished through

the use of a mapping table. This table consisted of a frame made of 4.5 x 4.5cm oak boards and a top made of a 0.5 x 0.5m piece of 0.6cm plexiglass. The legs of the table were 14cm long. The lower surface of the mapping window was held 20cm above the soil surface. In mapping, the table was positioned over a treatment, a 0.5 x 0.5m piece of acetate was laid on the surface of the table, and the position of each seedling present was recorded on the acetate in indelible ink. Seedlings of each species were coded by symbol and color. During each mapping period the seedlings present in each treatment of each experiment were recorded on separate acetate sheets. Whenever the height of the *Phleum pratense* lawn reached the lower surface of the mapping window, it was clipped to allow clear view of the seedlings to be mapped. Likewise when any bolting biennial reached the level of the mapping window, it was clipped and the fact of its bolting was recorded. At the conclusion of the study period, the acetate sheets for both experiments were processed.

E. Data analysis

Data from the soil texture and gap size experiments were analyzed on four levels. Initially the number of seedlings which successfully established in the two experiments were compared. Subsequently, each experiment was analyzed separately. The overall numbers of seedlings which were present on each sampling date in all treatments were expressed graphically. Within each treatment the number of seedlings present on each sampling date and the proportion of that number which was contributed by each species was presented graphically. Finally, the performance of each species was

evaluated both within and between treatments in each experiment. For the purpose of this evaluation the numbers of seedlings of each species which were present within a given treatment on a given sampling date were expressed as a proportion of the numbers of seeds of that species which were initially sown into that treatment. Since these are proportional data, they were transformed to angular values before further analysis (Sokal and Rohlf 1981).

After transformation, a series of one-way ANOVAs were performed among the four replicates of each treatment on each sampling date of both the soil texture and gap size experiments to determine whether there were significant differences in overall species response which resulted from the physical position of any of the replicates. The procedure used was the General Linear Model of the Statistical Analysis System (SAS 1982). Analyses failed to detect a significant difference ($P<0.05$) in the numbers of seedlings present between the four replicates of any treatment on any sampling date. Therefore, the number of seedlings of each species were pooled across the four replicates for each treatment on each sampling date to produce a mean number of seedlings present in that treatment. These mean values were used in subsequent analyses.

For multiple factorial ANOVAs performed to detect differences in the overall number of seedlings present between treatments and those performed to detect differences in the number of seedlings of a given species present between treatments, the data set was sorted by sampling date and the analysis was performed separately for each sampling date. Comparisons were made within each sampling date rather than between sampling dates. When

a significant difference was found, Tukey pairwise comparisons of the means were performed to find which means were significantly different.

6.3 Results

A. Overall comparison of the two experiments

Throughout both the soil texture and gap size experiments it was observed that, after sowing, seeds were moved to different locations within their section of the gradient box by wind and rainwash before they finally lodged, germinated, and the seedling emerged. In treatments in the soil texture experiment this movement resulted in many seedlings emerging near the walls of their section of the gradient box. In the gap size experiment however, a few seedlings emerged in the lawn outside of the gap where they had been sown. Emergence of seedlings outside of the gap was most prevalent among treatments in the two replicates adjacent to the fence which formed the eastern edge of the field station property. The number of seedlings which emerged in the lawn within a given replicate of treatments was never a sizeable proportion of the total number of seeds sown into those treatments. On the mid-June sampling date, when the spring flush of emergence was present, the maximum number of seedlings which emerged in the lawn around any treatment in any replicate was 1.2% of the seeds sown into that treatment. Since no significant difference ($P>0.05$) was found in the number of seedlings present in the gaps or treated area replicates of each treatment on each sampling date, those seedlings which emerged in the lawn outside of a gap were ignored for the purpose of subsequent analysis.

The numbers of seedlings of all species which were present at the end of the second growing season in each treatment are presented for the soil texture and the gap size experiments in Tables 6.3 and 6.4 respectively. The September 1983 sampling date was chosen for presentation because any seedling which had survived until the end of the growing season was considered to be successfully established. The number of seedlings present at this time could be used as a general measure of the relative success of the biennials in these two experiments.

Overall 40.0% more seedlings established in the gap size experiment than in the soil texture experiment. In the soil texture experiment the most seedlings established successfully in one part sand : one part gravel. Among the remaining treatments many more seedlings established on the two finer textures than on the two coarser textures. No seedlings emerged successfully in 100% gravel treatment. In the gap size experiment the largest number of seedlings emerged successfully in the largest gap and the number of seedlings which established decreased progressively with decreasing gap size. In the soil texture experiment *Daucus carota*, *Echium vulgare*, and *Melilotus* spp. made up 69.0% of the successfully established seedlings whereas in the gap size experiment *Arctium minus*, *Daucus carota*, and *Dipsacus sylvestris* made up 74.0% of the established seedlings.

Species	100% Sand	3:1	1:1	1:3	100% Gravel
Alliaria petiolata	2	5	14	19	0
Arctium minus	17	15	22	6	0
Cirsium vulgare	0	0	5	2	0
Daucus carota	58	50	77	31	0
Dipsacus sylvestris	14	10	7	10	0
Echium vulgare	67	79	89	68	0
Lactuca scariola	0	1	10	27	0
Melilotus spp.	21	35	44	3	0
Oenothera biennis	15	19	17	0	0
Onopordum acanthium	0	1	2	1	0
Tragopogon dubius	3	6	5	12	0
Tragopogon pratensis	3	3	0	5	0
Verbascum blattaria	0	0	0	0	0
Verbascum thapsus	0	2	3	0	0
Total	200	226	295	184	0

Table 6.3. Numbers of seedlings of 14 biennial taxa which successfully established (September 1983 sampling period) within each of 5 soil texture treatments summed over 4 replicates.

Species	40x40cm	30x30cm	20x20cm	10x10cm	No Gap
Alliaria petiolata	0	0	0	0	0
Arctium minus	128	101	53	37	77
Cirsium vulgare	29	27	21	2	7
Daucus carata	133	102	116	35	7
Dipsacus sylvestris	148	86	47	17	10
Echium vulgare	6	7	12	4	6
Lactuca scariola	0	1	1	0	0
Melilotus spp.	39	23	20	23	8
Oenothera biennis	5	1	3	0	0
Onopordum acanthium	0	0	1	0	0
Tragopogon dubius	8	7	7	4	0
Tragopogon pratensis	23	29	29	24	15
Verbascum blattaria	0	0	0	0	0
Verbascum thapsus	0	0	0	0	0
Total	519	384	310	146	130

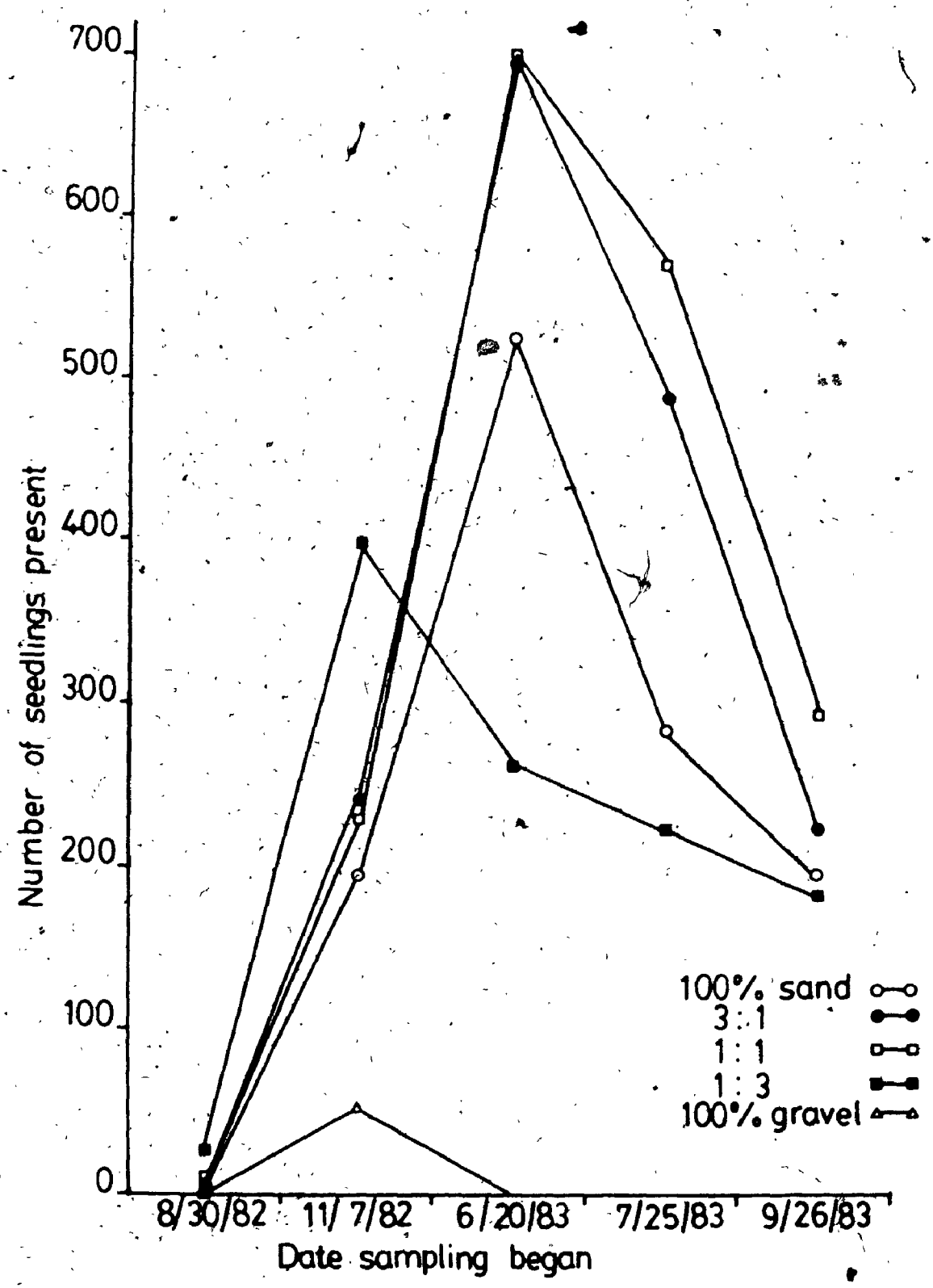
Table 6.4. Numbers of seedlings of 14 biennial taxa which successfully established (September 1983 sampling period) within each of 5 gap size treatments summed over 4 replicates.

B. Comparison between treatments within each experiment

1. Soil texture experiment

The overall number of seedlings which were present in each treatment of the soil texture experiment on each sampling date are presented in Figure 6.2. In the soil texture experiment seedlings were present in 100% gravel during the November 1982 sampling period only. In the 100% sand, 3:1 and 1:1 treatments the pattern in the number of seedlings present on each sampling date was similar, but the absolute numbers of seedlings present varied between treatments. All 3 treatments had very low numbers of seedlings present in August 1982 and more in November. There was a peak in June 1983 after spring emergence and a lower number of established seedlings present by September 1983. The 1:1 and 3:1 treatments had similar numbers of seedlings present during all sampling periods but the 100% sand treatment had lower numbers of seedlings present in June and July. In the 1:3 treatment the peak number of seedlings present was in the November 1982 sampling period and that number declined steadily. The number of seedlings which established successfully was greatest in the 1:1 treatment. Similar numbers were present in the remaining three treatments where establishment occurred.

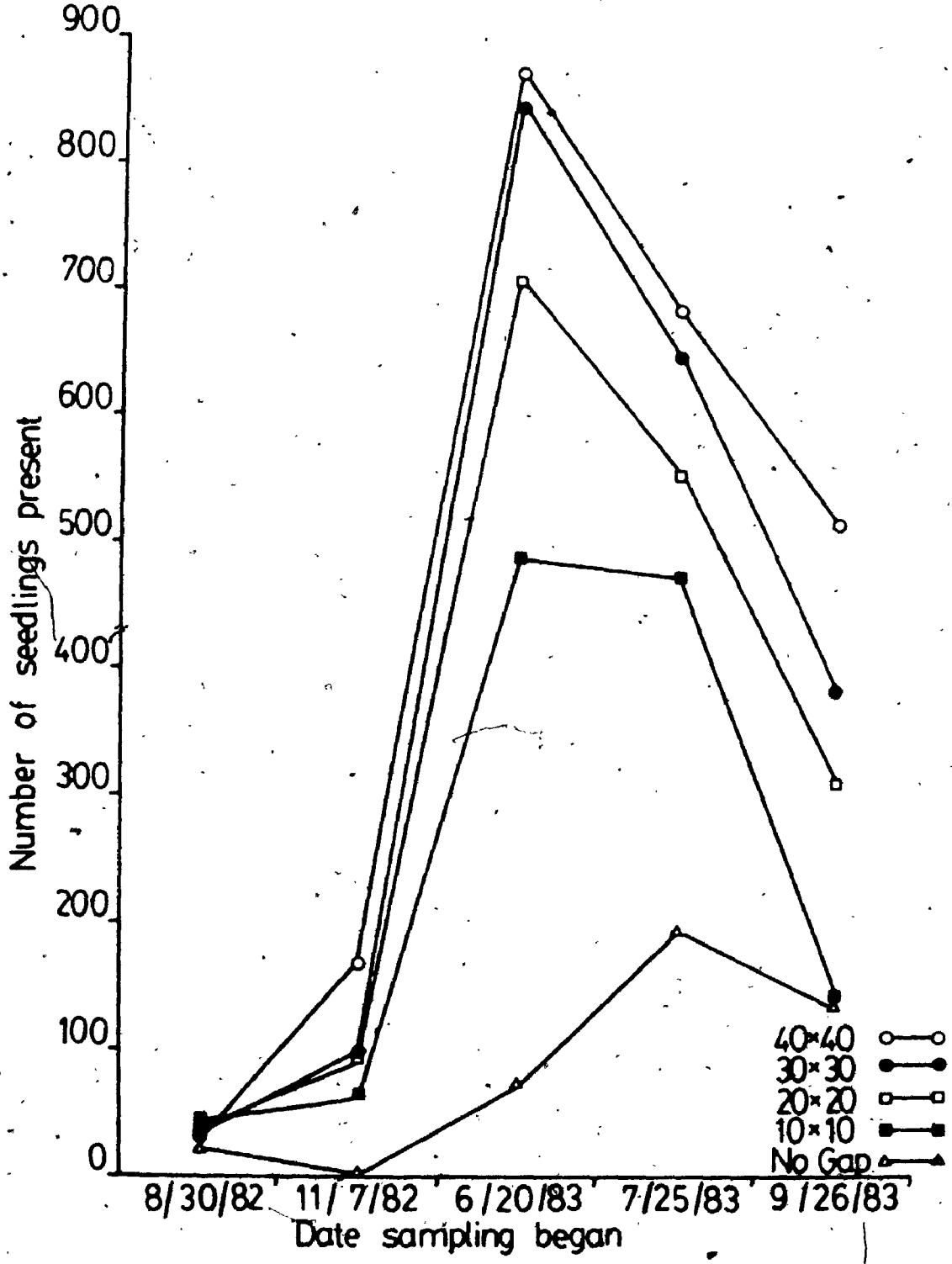
Figure 6.2. The numbers of seedlings of all biennial taxa which were present in each treatment in the soil texture experiment during 5 sampling periods.


700
600
500
400
300
200
100
0
Number of seedlings present
8/30/82
11/7/82
6/20/83
7/25/83
9/26/83
Date sampling began
100% sand
3:1
1:1
1:3
100% gravel

2. Gap size experiment

The overall number of seedlings which were present in each treatment of the gap size experiment is presented in Figure 6.3. In the gap size experiment, in all treatments except the control, there was a positive relationship between the size of the gap and the numbers of seedlings present on each sampling date. There were few seedlings present in any treatment during the August 1982 sampling period. By November a larger number of seedlings was present in the 40x40 cm gap than in any of the other 3 gaps. After the spring flush of emergence (June 1983 sampling period) there was a clear difference between treatments in the number of seedlings present. The 40x40 and 30x30cm gaps had by far the largest number, the 20x20cm gap had fewer and the 10x10cm gap had the fewest. In all 4 gap treatments there was a steep decline in numbers of seedlings present from June to September. In the 3 larger gaps this decline was continous through July, whereas in the 10x10cm gap the decline was most dramatic from July to September. In the no gap treatment numbers of seedlings present reached their peak in July and had declined by September. There was a clear difference between treatments in the number of seedlings which established. Most were in the 40x40cm gap and progressively fewer were present in each decreasing gap size. There was little difference between the number of seedlings which established in the 10x10cm gap and the number that established in the no gap treatment.

Figure 6.3. The numbers of seedlings of all biennial taxa which were present in each treatment in the gap size experiment during 5 sampling periods. Gap sizes were 40x40cm, 30x30cm, 20x20cm, 10x10cm and control (no gap).


900
800
700
600
500
400
300
200
100
0
Number of seedlings present
40×40
30×30
20×20
10×10
No Gap
8/30/82
11/7/82
6/20/83
7/25/83
9/26/83
Date sampling began

C. Comparison between sampling dates of each treatment within each experiment

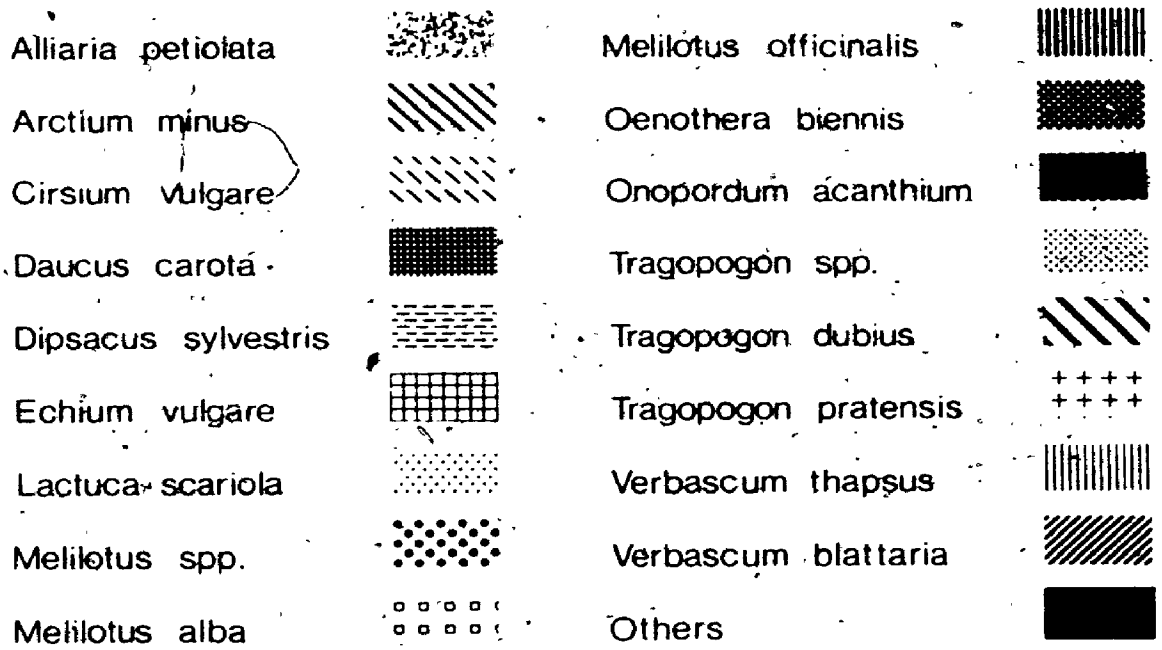
The numbers of seedlings which were present on each sampling date in each treatment of the soil texture experiment are presented in Figures 6.4 through 6.8 whereas those of the gap size experiment are presented in Figures 6.9 through 6.13. On each of these histograms the first bar represents the composition of the overall seed rain which was sown into all four replicates of that treatment. Subsequent bars show the relative proportions of seedlings of each species which were present on each sampling date. All species which made up more than 2.0% of the seedlings present in a given treatment on a given sampling date are identified independently in the bar, the rest are grouped as "others".

1. Soil texture experiment

In the 100% sand-treatment (Figure 6.4) 5 individuals of *Tragopogon dubius* were present in August. Many more seedlings were present in November (196) and 8 species were present in sufficient numbers to be noteworthy, especially *Daucus carota* (42.0%), *Echium vulgare* (16.0%) and *Verbascum thapsus* (22.0%). The spring flush of emergence resulted in the greatest number of seedlings of any sampling period (527), being present in June. Most of the seedlings of *Verbascum thapsus* however, failed to survive the winter. During the June sampling period 4 taxa, *Arctium minus* (10.0%), *Daucus carota* (30.0%), *Echium vulgare* (26.0%), and *Melilotus* spp. (13.0%) were particularly abundant. Also noteworthy in June was the appearance of seedlings of *Alliaria petiolata*, *Dipsacus sylvestris* and

Figure 6.4. Species composition of seed input and species composition of 18 biennial taxa which were present on 100% sand during 5 sampling periods. The number at the top of the first bar is the total number of seeds which was sown into the four replicates of that treatment. Numbers at the tops of the other five bars are the total numbers of seedlings which were present during those sampling periods.

KEY TO SPECIES SYMBOLS



COMPOSITION OF SEED INPUT AND SPECIES COMPOSITION OF EMERGED SEEDLINGS OF 15 BIENNIAL SPECIES WHICH WERE PRESENT ON 100 % SAND

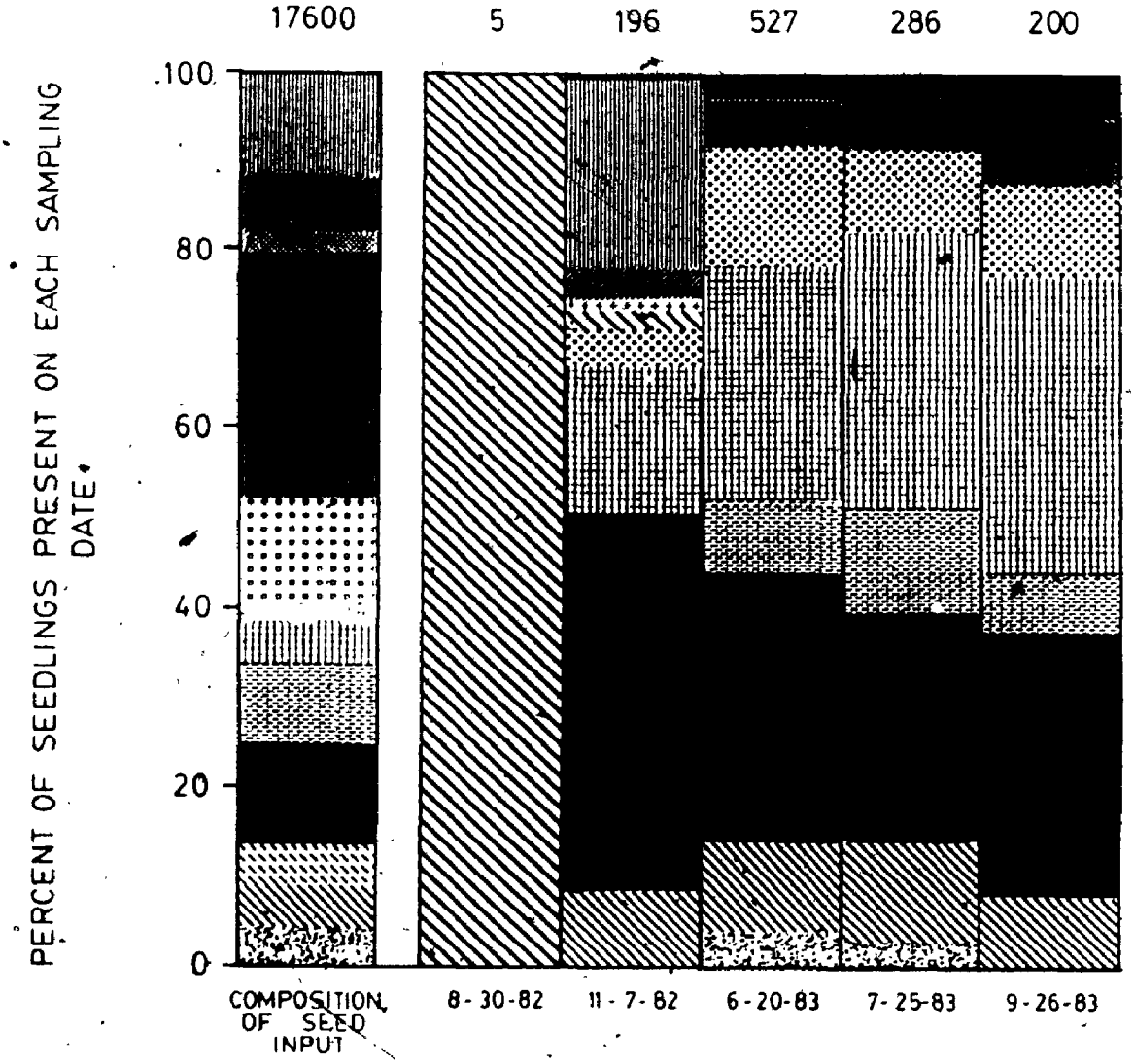
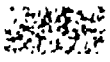
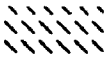
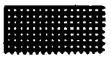
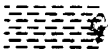
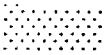
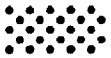
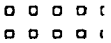


Figure 6.5. Species composition of seed input and species composition of 18 biennial taxa which were present on 75% sand/25% gravel during 5 sampling periods. The number at the top of the first bar is the total number of seeds which was sown into the four replicates of that treatment. Numbers at the tops of the other five bars are the total numbers of seedlings which were present during those sampling periods.

KEY TO SPECIES SYMBOLS

Alliaria petiolata		Melilotus officinalis	
Arctium minus		Oenothera biennis	
Cirsium vulgare		Onopordum acanthium	
Daucus carota		Tragopogon spp.	
Dipsacus sylvestris		Tragopogon dubius	
Echium vulgare		Tragopogon pratensis	
Lactuca scariola		Verbascum thapsus	
Melilotus spp.		Verbascum blattaria	
Melilotus alba		Others	

COMPOSITION OF SEED INPUT AND SPECIES COMPOSITION OF EMERGED SEEDLINGS OF 15 BIENNIAL SPECIES WHICH WERE PRESENT ON 75% SAND / 25% GRAVEL

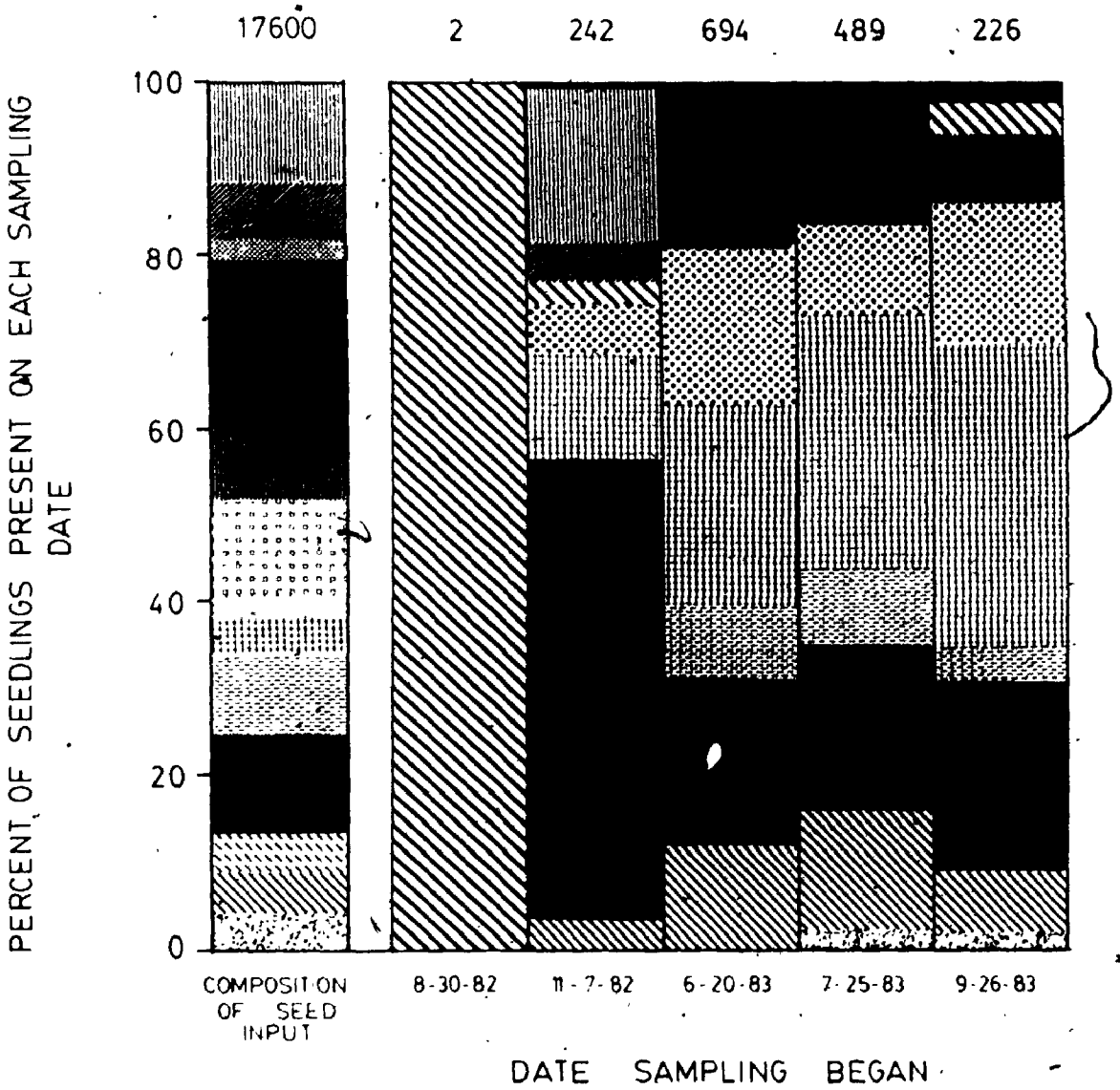
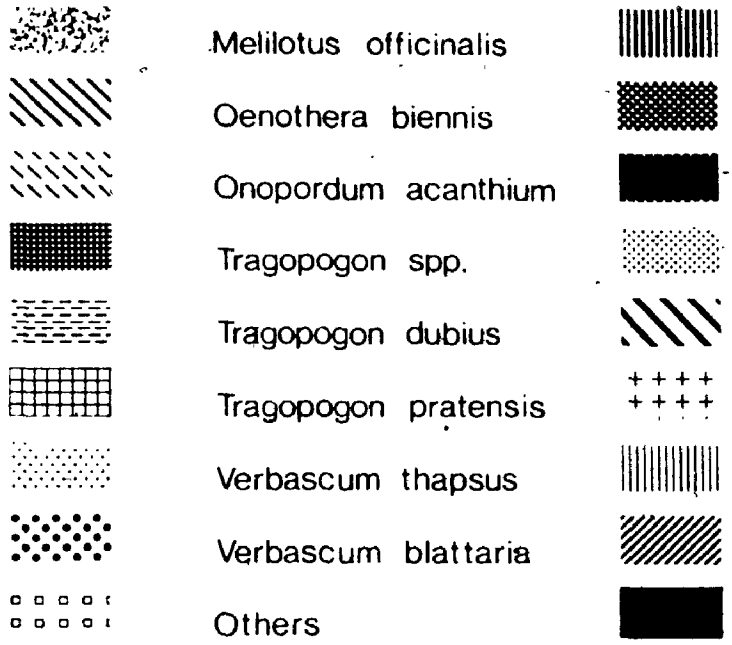


Figure 6.6. Species composition of seed input and species composition of 18 biennial taxa which were present on 50% sand/50% gravel during 5 sampling periods. The number at the top of the first bar is the total number of seeds which was sown into the four replicates of that treatment. Numbers at the tops of the other five bars are the total numbers of seedlings which were present during those sampling periods.

KEY TO SPECIES SYMBOLS



COMPOSITION OF SEED INPUT AND SPECIES COMPOSITION OF EMERGED SEEDLINGS OF 15 BIENNIAL SPECIES WHICH WERE PRESENT ON 50 % SAND / 50% GRAVEL

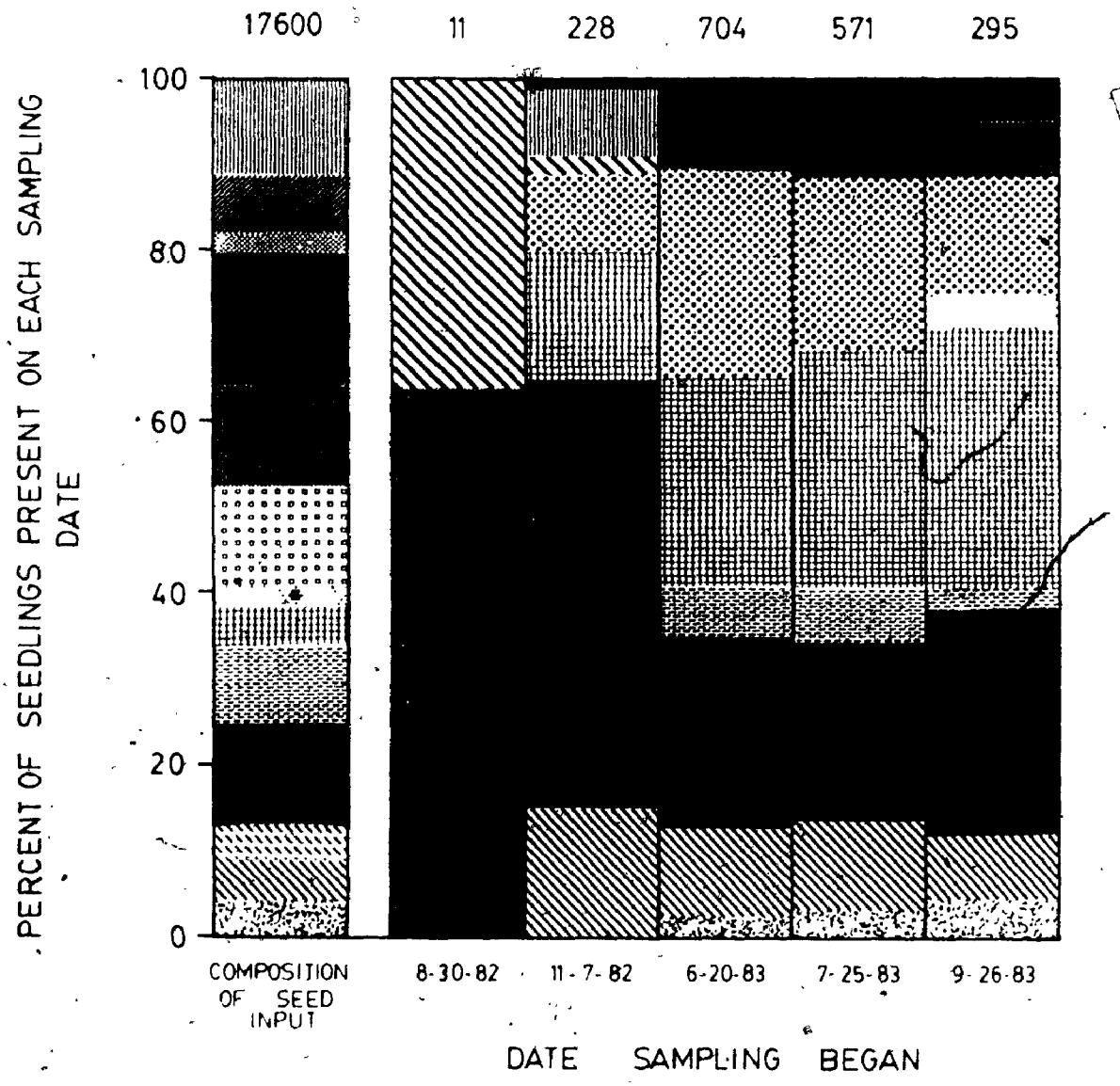
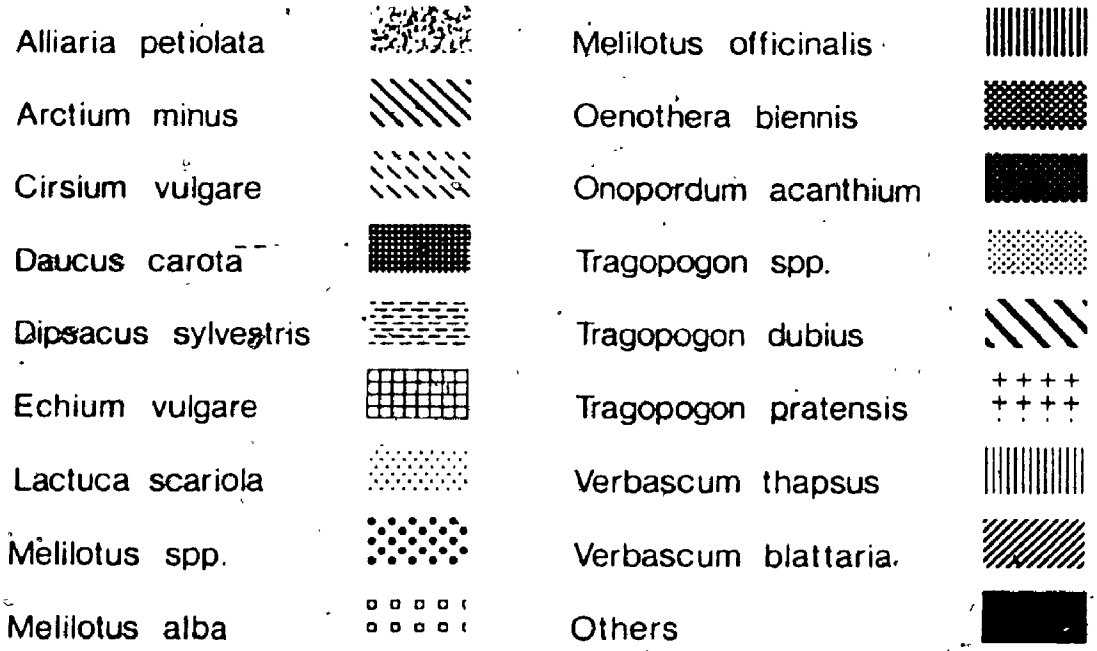


Figure 6.7. Species composition of seed input and species composition of 18 biennial taxa which were present on 25% sand/75% gravel during 5 sampling periods. The number at the top of the first bar is the total number of seeds which was sown into the four replicates of that treatment. Numbers at the tops of the other five bars are the total numbers of seedlings which were present during those sampling periods.

KEY TO SPECIES SYMBOLS



COMPOSITION OF SEED INPUT AND SPECIES COMPOSITION OF EMERGED SEEDLINGS OF 15 BIENNIAL SPECIES WHICH WERE PRESENT ON 25% SAND / 75% GRAVEL

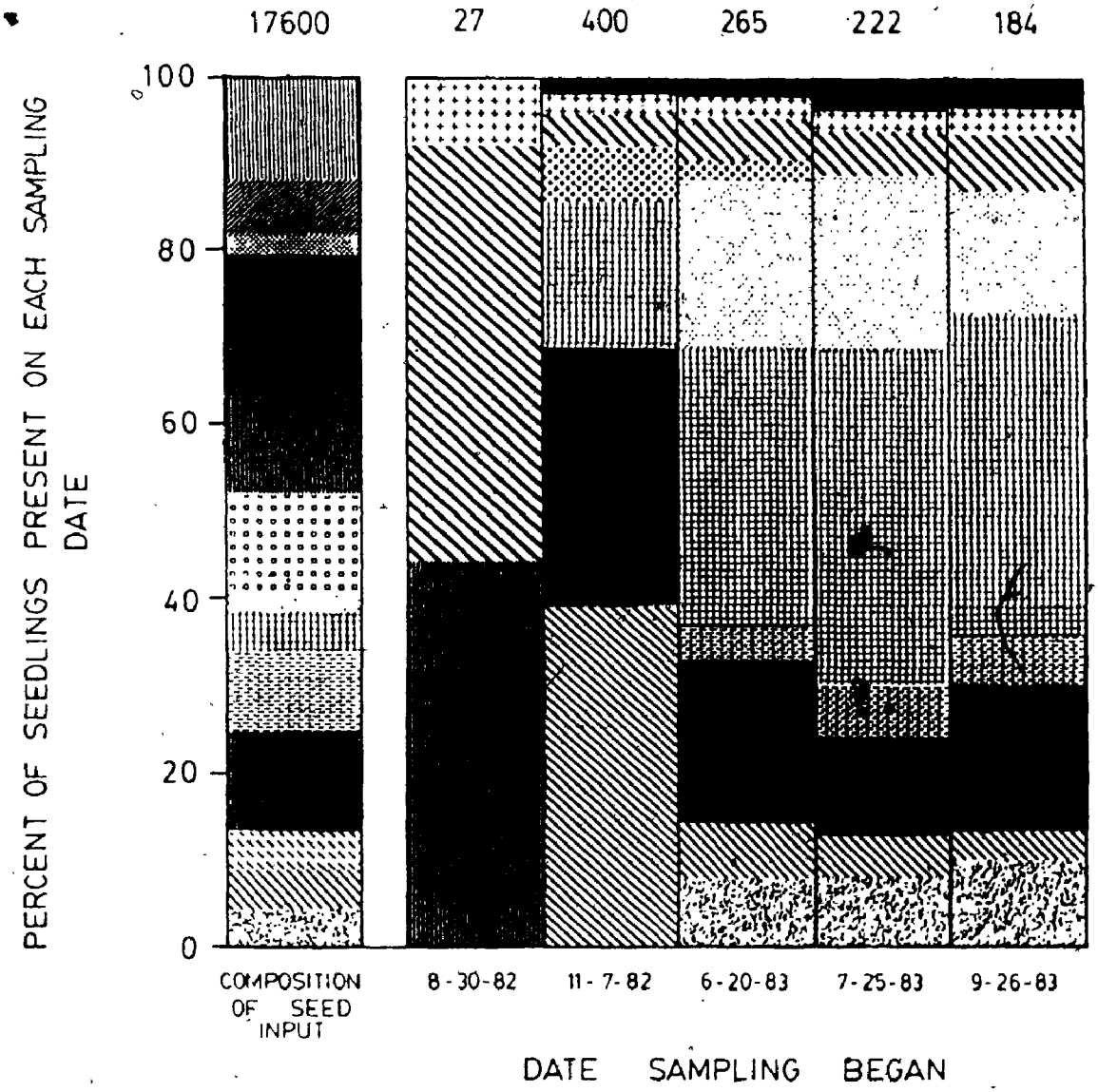
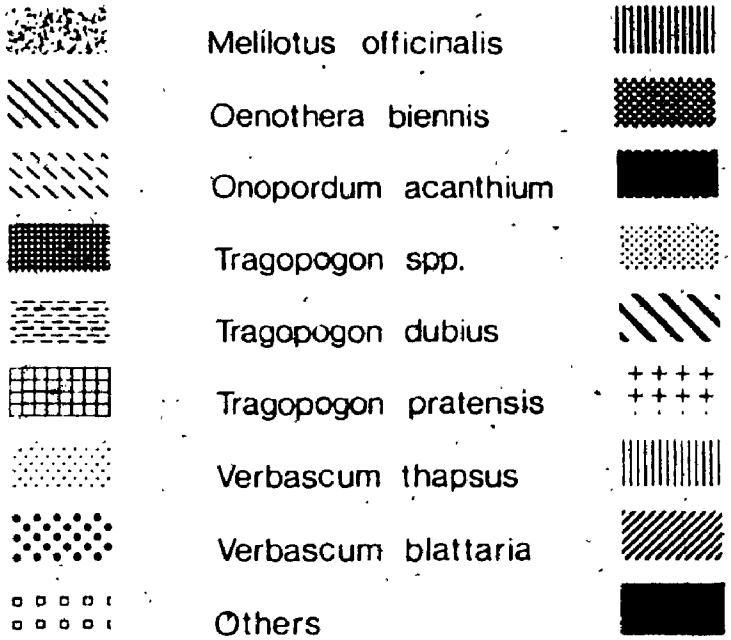


Figure 6.8. Species composition of seed input and species composition of 18 biennial taxa which were present on 100% gravel during 5 sampling periods. The number at the top of the first bar is the total number of seeds which was sown into the four replicates of that treatment. Numbers at the tops of the other five bars are the total numbers of seedlings which were present during those sampling periods.

KEY TO SPECIES SYMBOLS



COMPOSITION OF SEED INPUT AND SPECIES COMPOSITION OF EMERGED SEEDLINGS OF 15 BIENNIAL SPECIES WHICH WERE PRESENT ON 100 % GRAVEL

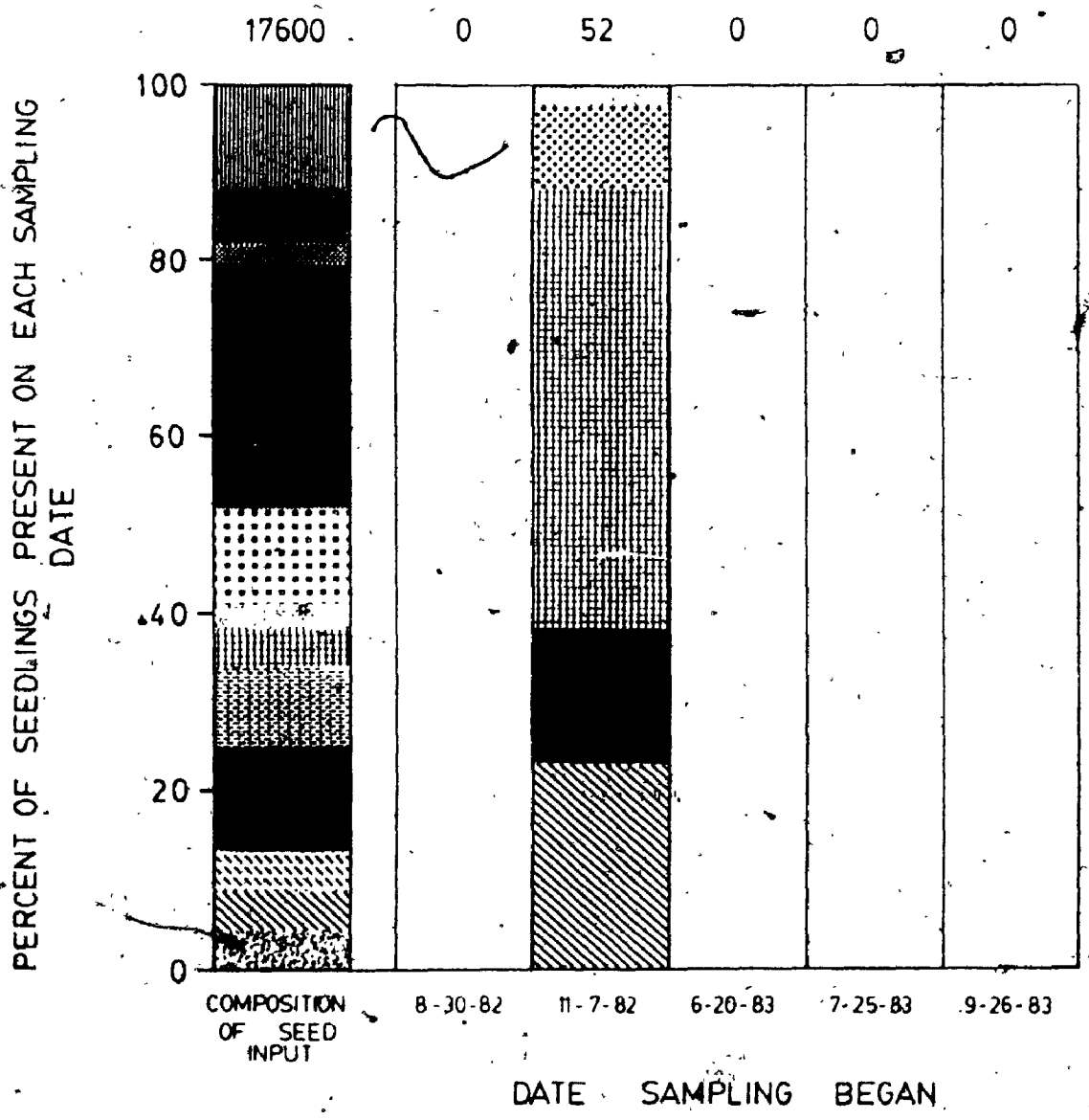
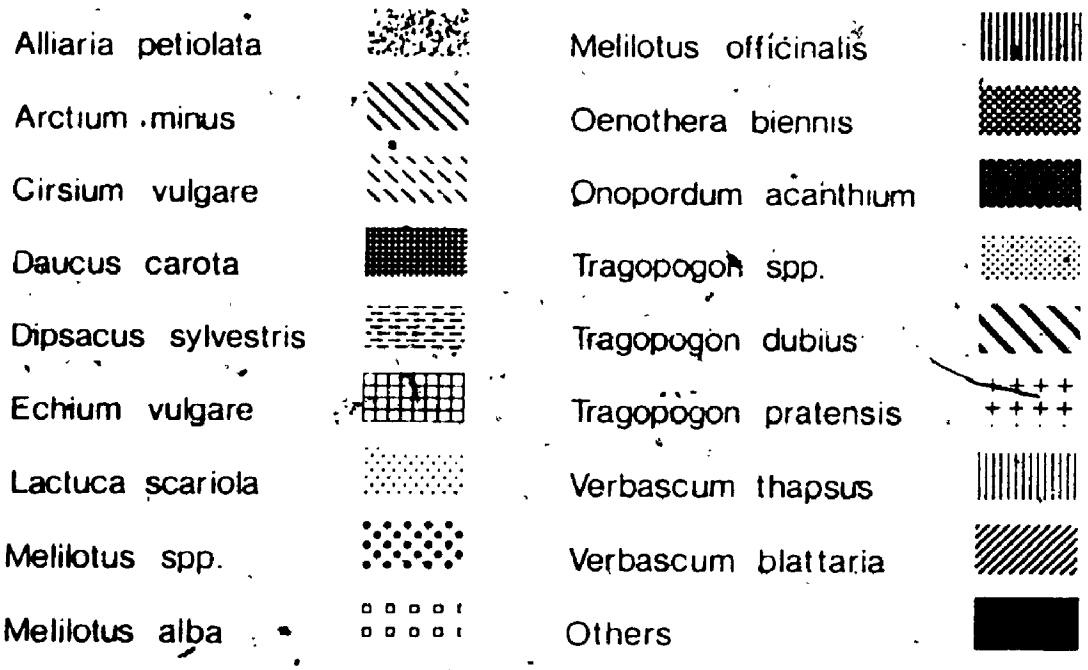


Figure 6.9. Species composition of seed input and species composition of 18 biennial taxa which were present within 40 X 40cm gaps during 5 sampling periods. The number at the top of the first bar is the total number of seeds which was sown into the four replicates of that treatment. Numbers at the tops of the other five bars are the total numbers of seedlings which were present during those sampling periods.

KEY TO SPECIES SYMBOLS



COMPOSITION OF SEED INPUT AND SPECIES COMPOSITION OF EMERGED SEEDLINGS OF 15 BIENNIAL SPECIES WHICH WERE PRESENT WITHIN 40 CM x 40 CM GAPS

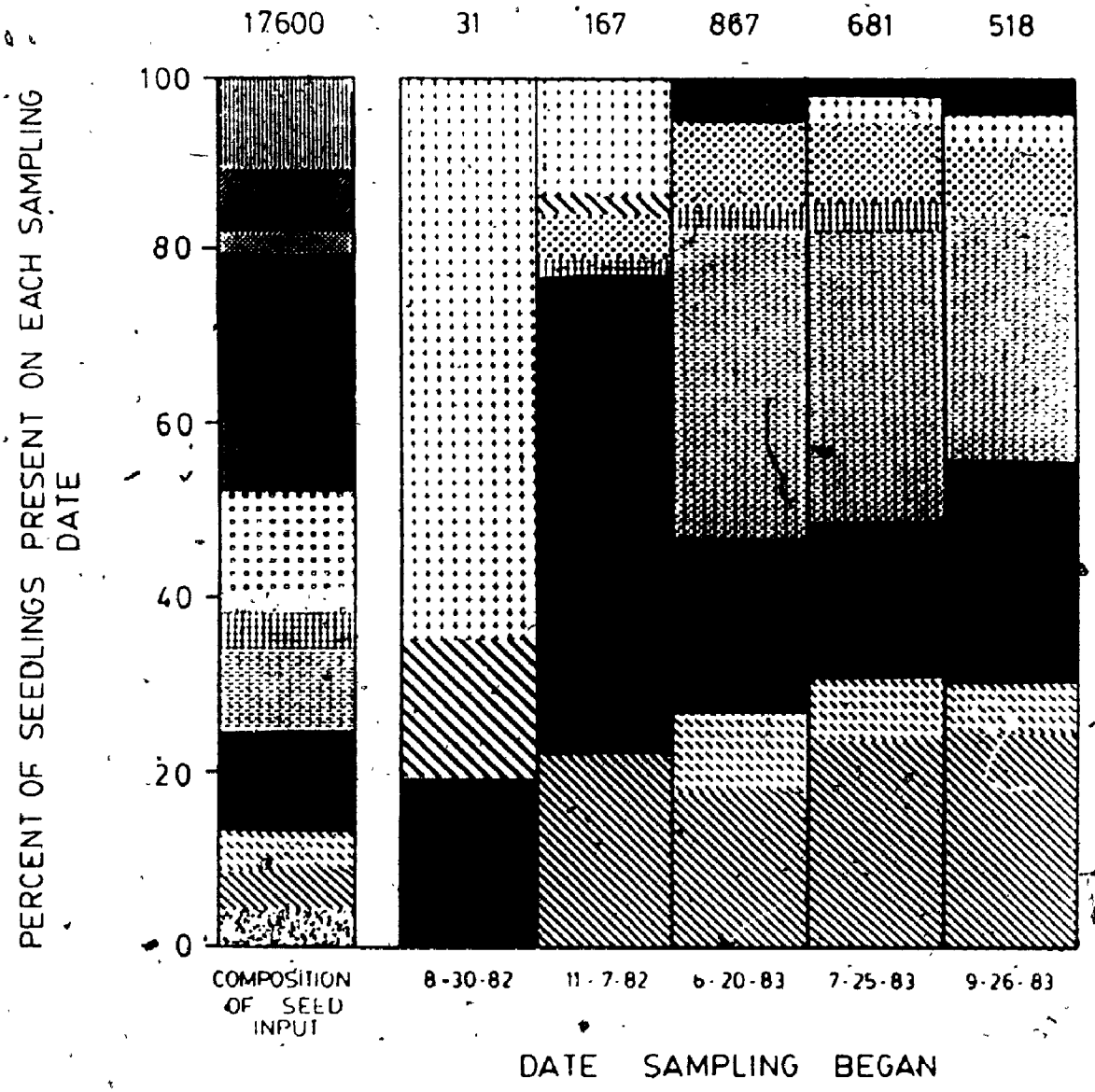
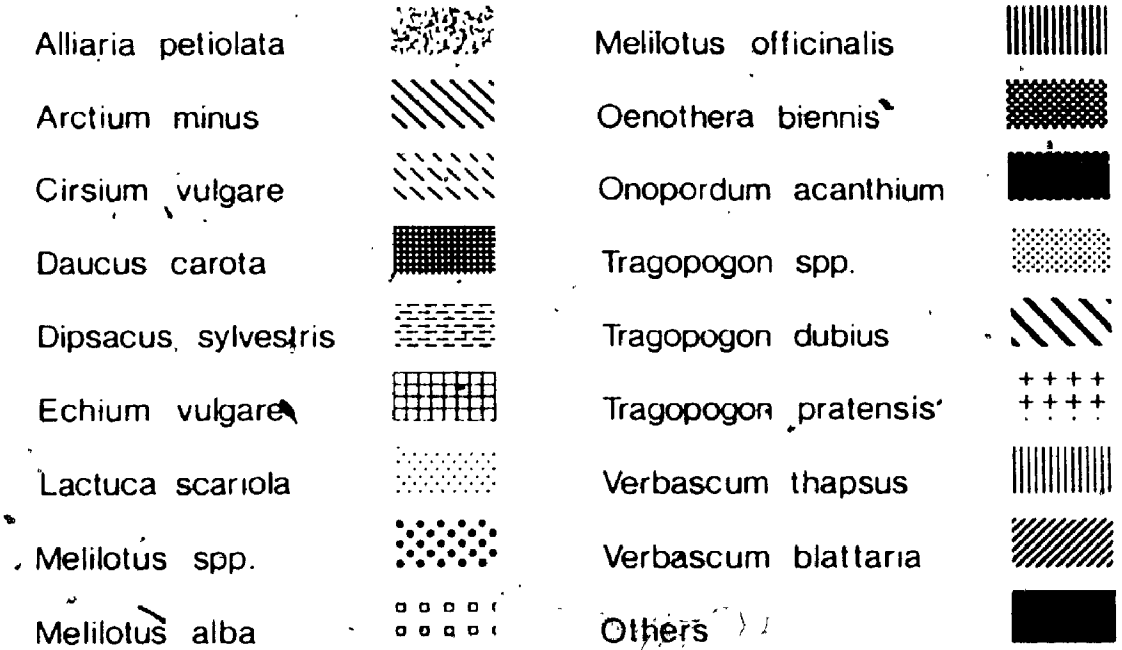


Figure 6.10. Species composition of seed input and species composition of 18 biennial taxa which were present within 30 X 30cm gaps during 5 sampling periods. The number at the top of the first bar is the total number of seeds which was sown into the four replicates of that treatment. Numbers at the tops of the other five bars are the total numbers of seedlings which were present during those sampling periods.

KEY TO SPECIES SYMBOLS



COMPOSITION OF SEED INPUT AND SPECIES COMPOSITION OF EMERGED SEEDLINGS OF 15 BIENNIAL SPECIES WHICH WERE PRESENT WITHIN 30 CM x 30 CM GAPS

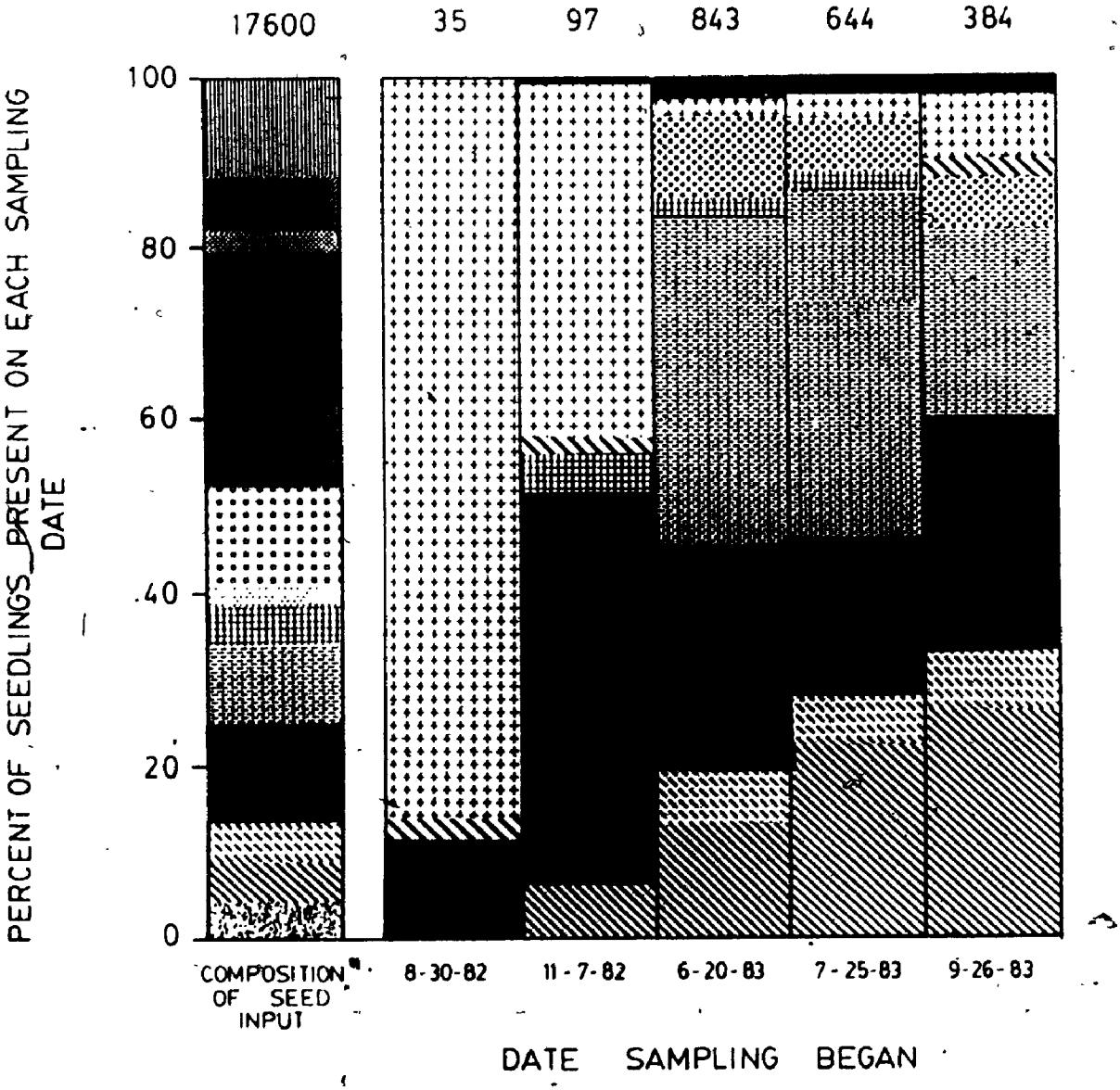
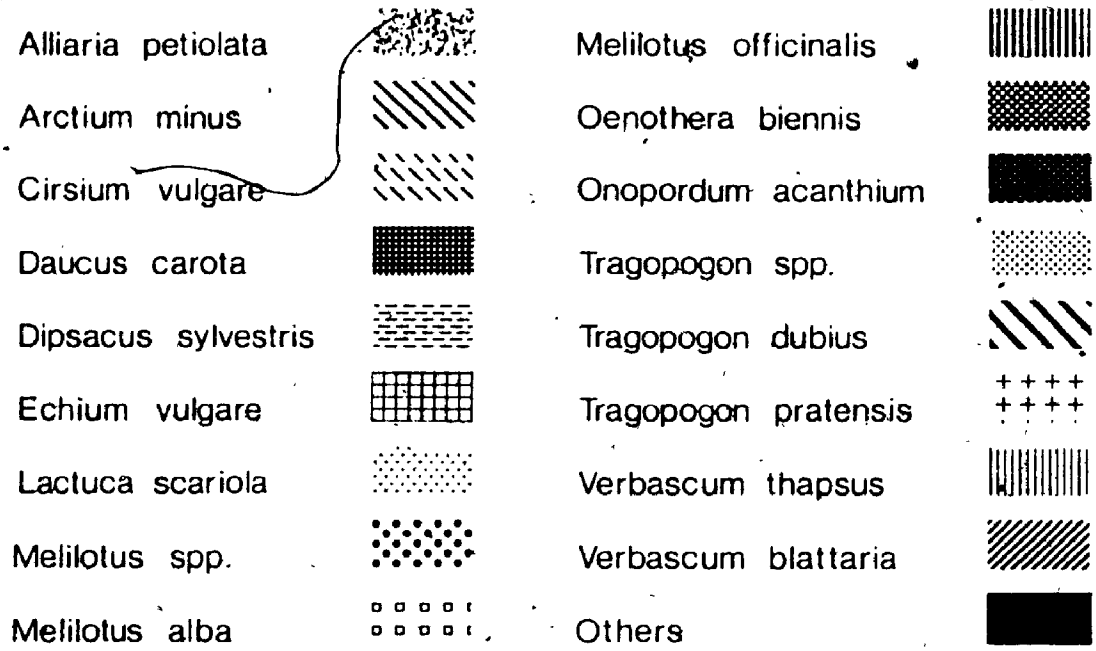


Figure 6.11. Species composition of seed input and species composition of 18 biennial taxa which were present within 20 X 20cm gaps during 5 sampling periods. The number at the top of the first bar is the total number of seeds which was sown into the four replicates of that treatment. Numbers at the tops of the other five bars are the total numbers of seedlings which were present during those sampling periods.

KEY TO SPECIES SYMBOLS



COMPOSITION OF SEED INPUT AND SPECIES COMPOSITION OF EMERGED SEEDLINGS OF 15 BIENNIAL SPECIES WHICH WERE PRESENT WITHIN 20 CM x 20 CM GAPS

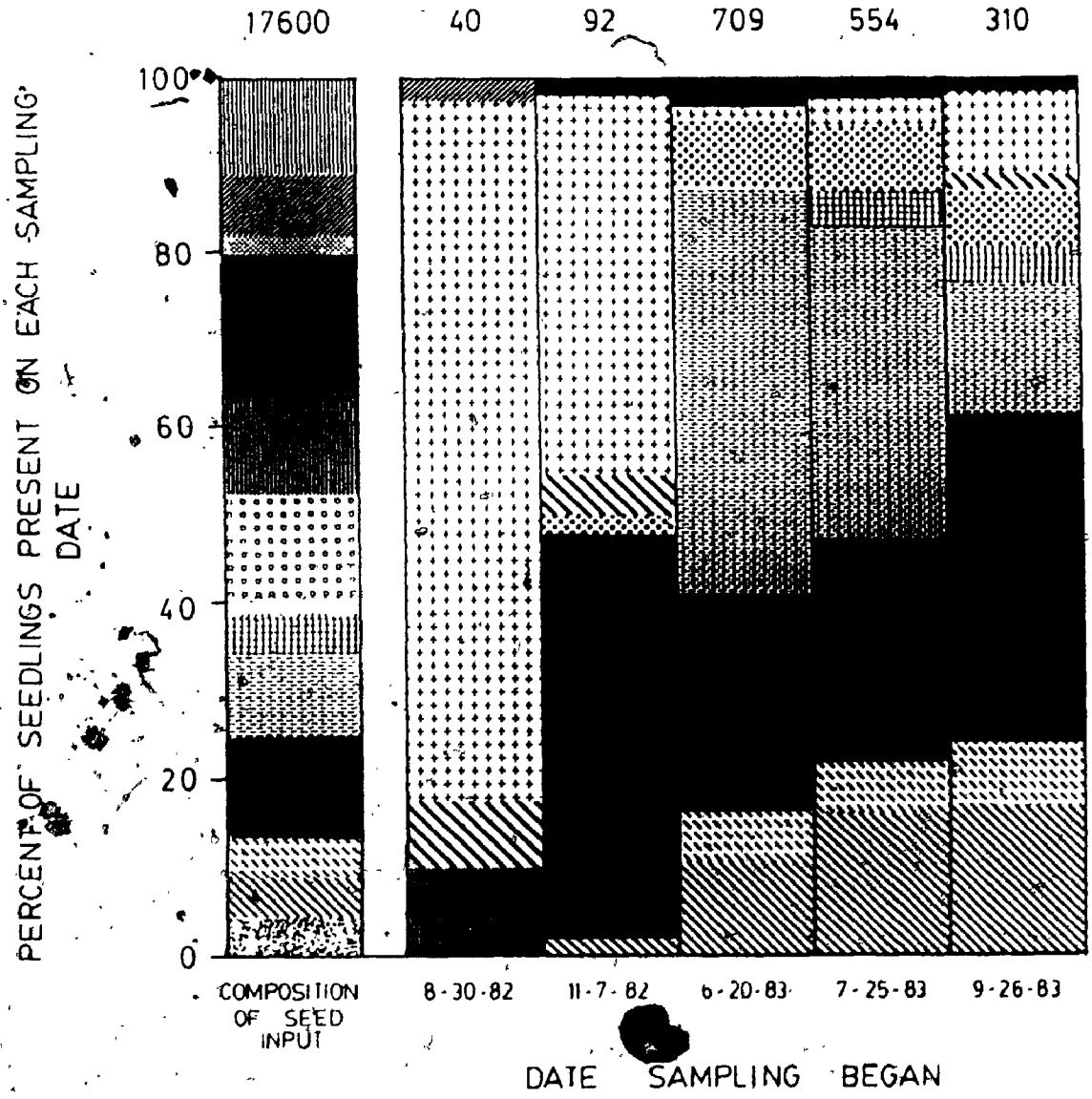
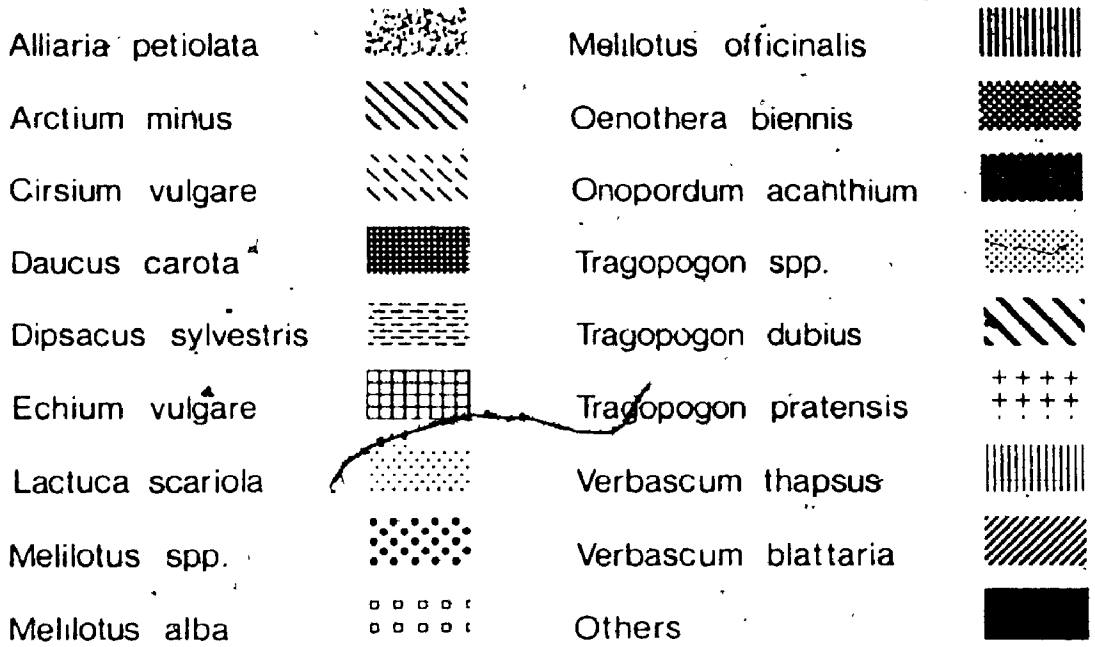


Figure 6.12. Species composition of seed input and species composition of 18 biennial taxa which were present within 10 X 10cm gaps during 5 sampling periods. The number at the top of the first bar is the total number of seeds which was sown into the four replicates of that treatment. Numbers at the tops of the other five bars are the total numbers of seedlings which were present during those sampling periods.

KEY TO SPECIES SYMBOLS



COMPOSITION OF SEED INPUT AND SPECIES COMPOSITION OF EMERGED SEEDLINGS OF 15 BIENNIAL SPECIES WHICH WERE PRESENT WITHIN 10 CM x 10 CM GAPS

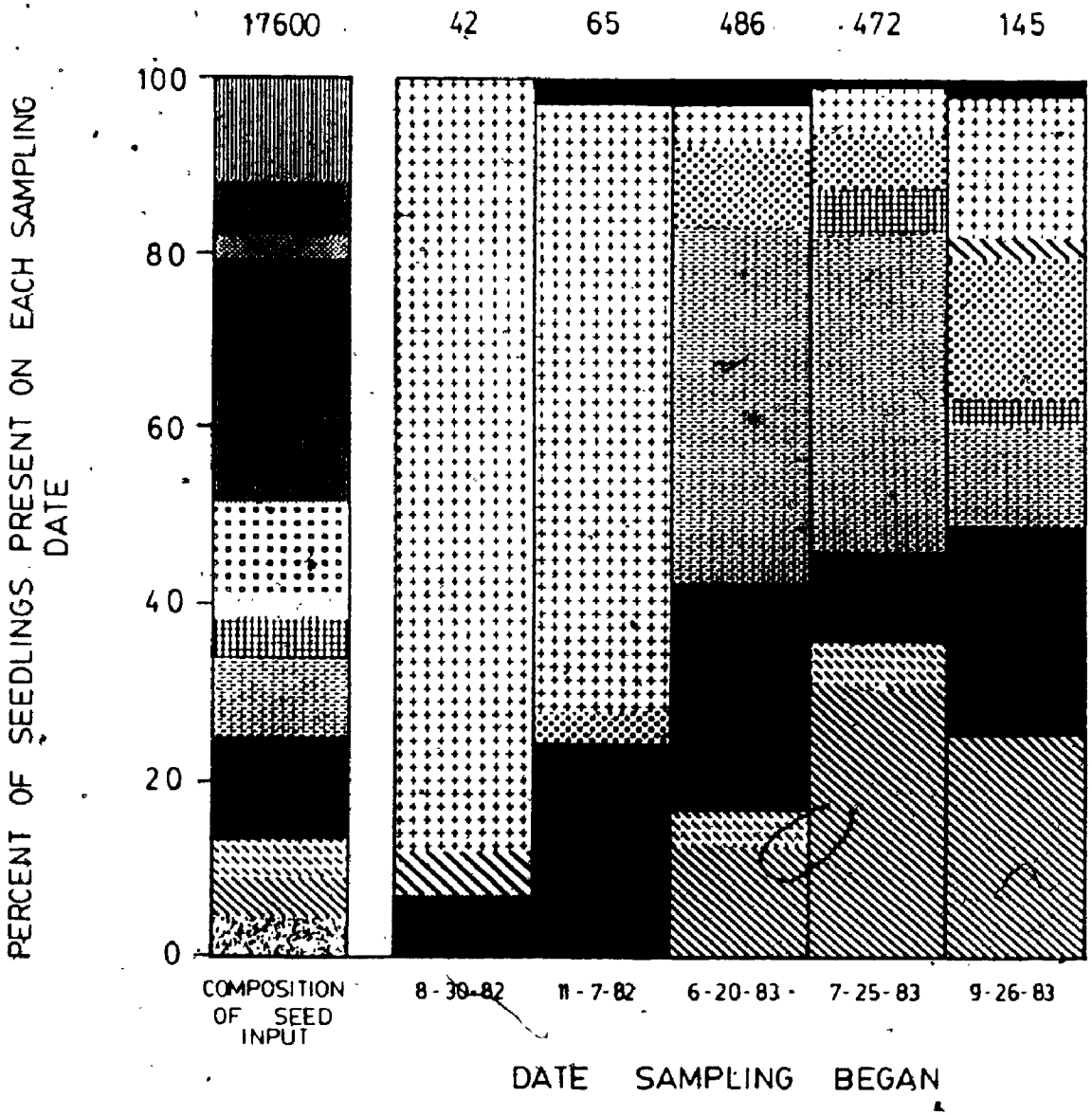
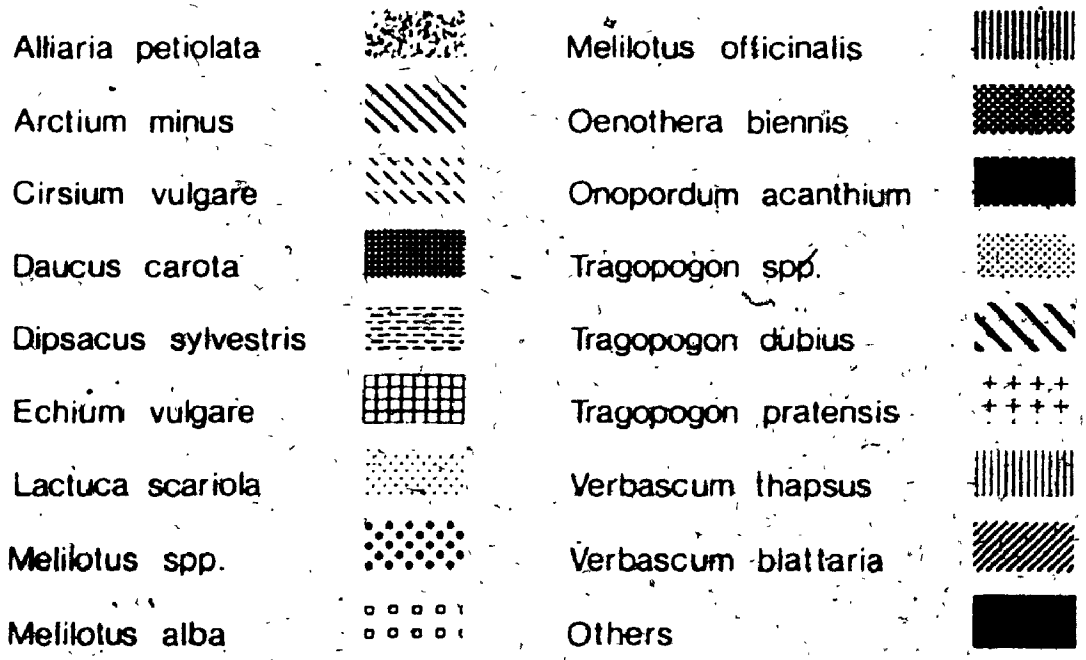
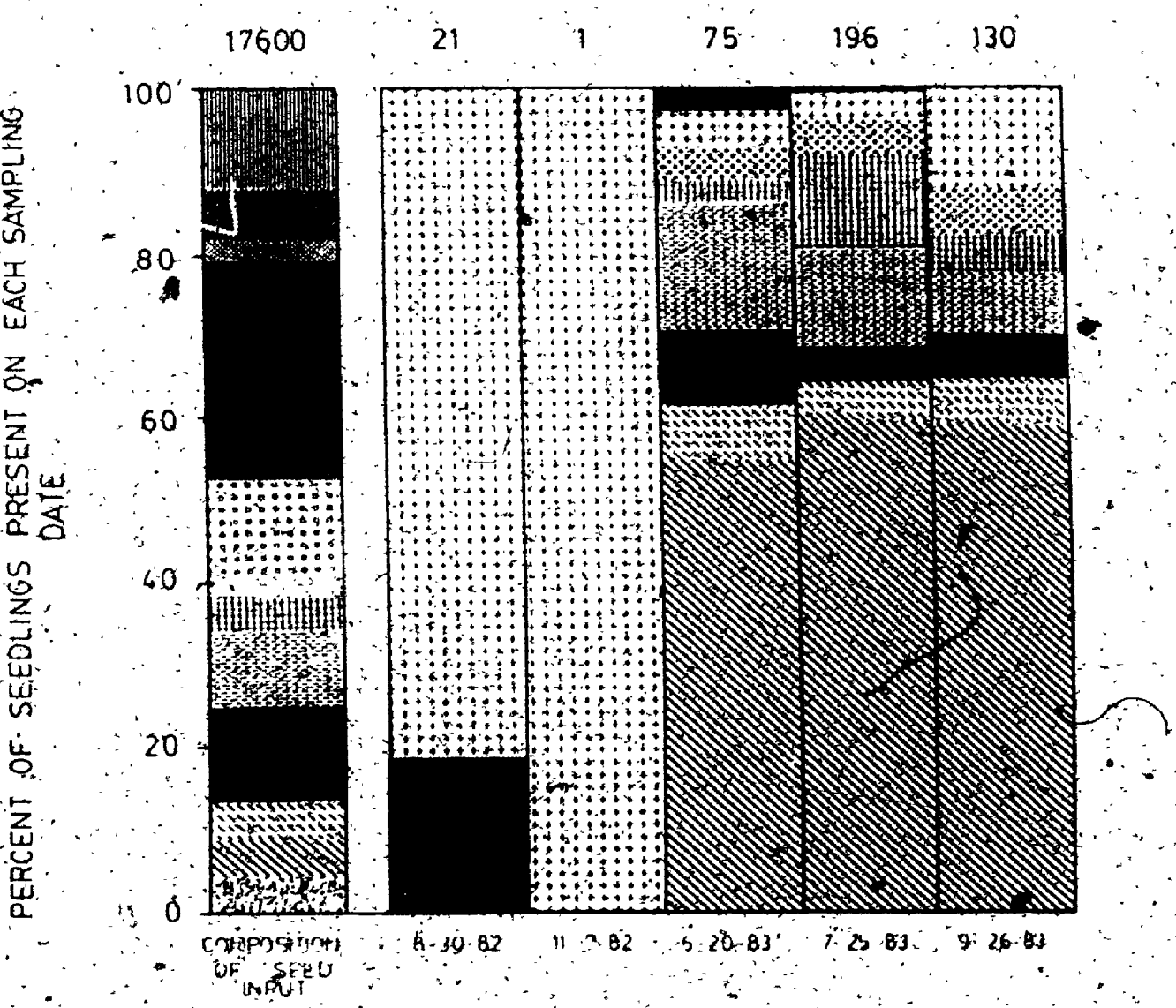


Figure 6.13. Species composition of seed input and species composition of 18 biennial taxa which were present within a lawn of *Phleum pratense* L. during 5 sampling periods. The number at the top of the first bar is the total number of seeds which was sown into the four replicates of that treatment. Numbers at the tops of the other five bars are the total numbers of seedlings which were present during those sampling periods.

KEY TO SPECIES SYMBOLS



COMPOSITION OF SEED INPUT AND SPECIES COMPOSITION OF EMERGED SEEDLINGS OF 15 BIENNIAL SPECIES WHICH WERE PRESENT WITHIN A LAWN OF PHLEUM PRATENSE L.



Oenothera biennis. Although the absolute numbers of seedlings present in this treatment declined through July (268) and had declined again by the September sampling period (200), all of the species present in June remained at approximately their same relative proportions except for *Alliaria petiolata* whose numbers of successfully established seedlings dwindled to insignificance.

In the 3:1 treatment (Figure 6.5) only two individuals, both *Tragopogon dubius*, were present in August. Many more seedlings were present in November (242) and seven species were present in sufficient numbers to be noteworthy. Of these, *Daucus carota* (53.0%), *Echium vulgare* (12.0%), and *Verbascum thapsus* (18.0%), made up 83.0% of the seedlings present. The spring flush of emergence resulted in the greatest number of seedlings being present in June (694). Most of the *Verbascum thapsus* seedlings failed to survive the winter. During this sampling period 5 species made up 85.0% of the seedlings present, namely *Arctium minus*, *Daucus carota*, *Echium vulgare*, *Melilotus* spp., and *Oenothera biennis*. The absolute numbers of seedlings present in this treatment had declined by the July sampling period (489). Three of the species which were numerous in June remained in relatively similar proportions, but *Echium vulgare* increased to 29.0% and *Melilotus* spp. declined to 10.0%. The number of established seedlings was substantially smaller (226) in September than that present in July and the relative proportions of the species present had changed. *Arctium minus* and *Oenothera biennis* declined to 7.0 and 8.0% respectively whereas *Daucus carota* remained approximately the same and *Echium vulgare* and *Melilotus* spp. increased to 36.0% and 15.0% respectively.

In the 1:1 treatment (Figure 6.6) a few individuals of *Melilotus officinalis* and *Tragopogon dubius* were present in August (11). Many more individuals were present in November (228) and 6 species were present in sufficient numbers to be noteworthy. Of these, 3 species, *Arctium minus*, *Daucus carota*, and *Echium vulgare* made up 80.0% of the seedlings present. The spring flush of emergence resulted in the largest number of seedlings being present in June (704). The numerous species were *Arctium minus* (10.0%), *Daucus carota* (22.0%), *Echium vulgare* (24.0%), and *Melilotus* spp. (24.0%). By the July sampling period, the absolute number of seedlings present had declined (571) but their relative proportions were approximately the same as they had been in June. Two hundred and ninety-five seedlings successfully established in this treatment. Of these, 3 taxa made up 71.0% of the seedlings present. They were *Daucus carota* (26.0%), *Echium vulgare* (30.0%), and *Melilotus* spp. (15.0%).

In the 1:3 treatment (Figure 6.7) 27 seedlings emerged in August. Of these 44.0% were *Melilotus officinalis* and 48.0% were *Tragopogon dubius*. The largest number of seedlings present on any sampling date in this treatment was recorded in November (400). Of these, 3 species made up 86.0% of the seedlings present, *Arctium minus*, *Daucus carota*, and *Echium vulgare*. There was a substantial decline in the numbers of seedlings present in June (265). However, 9 species were present in large enough numbers to be noteworthy, especially *Daucus carota* (18.0%), *Echium vulgare* (32.0%), and *Lactuca scariola* (20.0%). There was a slight decline in the absolute numbers of seedlings present in July (222). The relative proportions of the seedlings present remained constant for all species except for *Echium vulgare* which

had increased to 37.0% and *Daucus carota* which had declined to 11.0%. There were 184 seedlings which successfully established in this treatment. The most numerous species were *Alliaria petiolata* (10.0%), *Daucus carota* (17.0%), *Echium vulgare* (37.0%), and *Lactuca scariola* (15.0%).

In the 100% gravel treatment (Figure 6.8) no seedlings were present until the November sampling date when there were 52 present, primarily *Arctium minus* (23.0%), *Daucus carota* (15.0%), *Echium vulgare* (50.0%), and *Melilotus* spp. (10.0%). No seedlings were present on any subsequent sampling date.

2. Gap size experiment

In the 40x40cm gap treatment (Figure 6.9) 31 seedlings were present during the August sampling period. Of these *Melilotus officinalis* made up 20.0%, *Tragopogon dubius* 15.0%, and *Tragopogon pratensis* 65.0%. The number of seedlings present increased to 167 by November. Of these, 3 species (*Arctium minus* (22.0%), *Daucus carota* (55.0%), and *Tragopogon pratensis*) made up 91.0% of the seedlings present. The spring flush of emergence resulted in the greatest number of seedlings (867) being present in June. The absolute numbers of seedlings had declined to 681 by July and to 518 by November. Three species were dominant at each of these sampling periods, namely *Arctium minus*, *Daucus carota*, and *Dipsacus sylvestris*.

In the 30x30cm gap treatment (Figure 6.10) 35 seedlings were present during the August sampling period, mostly *Tragopogon pratensis*. By November the *Tragopogon pratensis* seedlings were matched by an almost

equal number of *Daucus carota* seedlings. The spring flush of emergence resulted in the largest number of seedlings being present in June. Four species made up 87.0% of the seedlings present, namely *Arctium minus* (13.0%), *Daucus carota* (26.0%), *Dipsacus sylvestris* (38.0%), and *Melilotus* spp. (10.0%). The number of seedlings present declined by July (644). Three hundred and eighty-four seedlings successfully established in this treatment. Of these 3 species made up 75.0% of the seedlings present (*Arctium minus*, *Daucus carota*, and *Dipsacus sylvestris*).

In the 20x20cm gap treatment (Figure 6.11) 40 seedlings were present during the August sampling date. Of these 80.0% were *Tragopogon pratensis*. More seedlings (92) were present by November with most seedlings being *Daucus carota* and with *Tragopogon pratensis* numbers being maintained. The spring flush of emergence resulted in more seedlings (709) at the June sampling date than at any other time. Of these, *Dipsacus sylvestris* increased dramatically to nearly half the total (46.0%). The absolute number of seedlings present had declined by July, and by November 310 had successfully emerged in this treatment. Eight species were numerous enough to be noteworthy at the final count with *Arctium minus* (17.0%), *Daucus carota* (38.0%), and *Dipsacus sylvestris* (15.0%) being most abundant.

In the 10x10cm gap treatment (Figure 6.12) 42 seedlings were present in the August sampling period. Of these 86.0% were *Tragopogon pratensis*. Sixty-five seedlings were present by November, primarily *Daucus carota* (25.0%) and *Tragopogon pratensis* (70.0%). The spring flush of germination resulted in the largest number of seedlings being present (486) in June. Of these 4 taxa made up 89.0%, *Arctium minus*, *Daucus carota*, *Dipsacus*

sylvestris, and *Melilotus* spp.. There was only a slight reduction in numbers of individuals present by July (472). There was however a shift in the proportions of species present. *Daucus carota* remained at approximately the same proportion to that in June, but *Dipsacus sylvestris* was reduced to 10.0% and *Arctium minus* increased to 30.0%. One hundred and forty-five seedlings successfully established in this treatment. Five taxa made up 93.0% of the seedlings present, *Arctium minus* (25.0%), *Daucus carota* (23.0%), *Dipsacus sylvestris* (12.0%), *Melilotus* spp. (16.0%), and *Tragopogon pratensis* (17.0%).

In the no gap treatment (Figure 6.13) 21 seedlings were present during the August sampling period. Of these 81.0% were *Tragopogon pratensis*. Only one seedling was present in November; it was *Tragopogon pratensis*. Many more seedlings (75) were present by June, after the spring flush of germination. Of these, *Arctium minus* (55.0%), *Daucus carota* (10.0%), and *Dipsacus sylvestris* (16.0%) were most numerous. The largest number of seedlings present in this treatment (196) occurred in July. The most common species were *Arctium minus* (60.0%), *Dipsacus sylvestris* (12.0%), and *Echium vulgare* (12.0%). One hundred and thirty seedlings successfully established in this treatment. More than two-thirds were *Arctium minus* (59.0%) and *Tragopogon pratensis* (12.0%).

D. Performance of each species in all treatments on each sampling date in each experiment

Appendix I compares the mean percentage of seedlings present between the 5 soil texture treatments during each of 5 sampling periods for each species. Table 6.5 compares the mean percentage of seedlings of each species which successfully established in each treatment of the soil texture experiment. Appendix II compares the mean percentage of seedlings present between the 5 gap size treatments during each of 5 sampling periods for each species. Table 6.6 compares the mean percentage of seedlings of each species which successfully established in each treatment of the gap size experiment.

1. Soil texture experiment

The percentage of seeds of each species which were present as established seedlings (by November 1983) within each treatment in the soil texture experiment are compared in Table 6.5. The greatest number of species (12) was present in the 1:1 treatment. No seedlings of any species were able to establish in the 100% gravel treatment, so the remainder of this paragraph will involve only the other four treatments. In the 100% sand treatment, the only species which had a percentage emergence significantly ($P<0.05$) greater than 0 were *Daucus carota* and *Echium vulgare*, but they were not different from one another. Five species, *Cirsium vulgare*, *Lactuca scariola*, *Onopordum acanthium*, *Verbascum blattaria*, and *Verbascum thapsus* had no seedlings establish in this treatment. In the 3:1 treatment *Echium vulgare* had a significantly larger ($P<0.05$) percentage of established

Table 6.5. Comparison of the mean percentage (± S.D.) of seedlings of each of 15 biennial taxa which established within each of 5 soil textures. Values for each taxa are expressed as a percentage of the number of seeds initially sown. Entries within a column followed by the same letter are not significantly different (P>0.05).

Species	100% Sand	3:1	1:1	1:3	100% Gravel
Alliaria petiolata	0.2 ± 0.3bc	0.8 ± 1.2bc	1.8 ± 0.9bcd	2.4 ± 2.4abc	0a
Arctium minus	2.1 ± 1.7bc	1.5 ± 0.9bc	2.8 ± 1.6bc	0.8 ± 1.5bc	0a
Cirsium vulgare	0c	0c	0.6 ± 1.0bcd	0.2 ± 0.5c	0a
Daucus carota	2.9 ± 1.5ab	2.3 ± 0.5b	3.8 ± 0.6ab	4.6 ± 1.0abc	0a
Dipsacus sylvestris	0.9 ± 0.8bc	0.6 ± 0.5bc	0.4 ± 0.6cd	0.6 ± 0.8bc	0a
Echium vulgare	8.4 ± 3.3a	10.1 ± 1.4a	11.1 ± 3.9a	8.5 ± 1.7a	0a
Lactuca scariola	0c	0.2 ± 0.5bc	2.5 ± 1.7bcd	6.8 ± 5.6a	0a
Melilotus spp.	0.5 ± 0.4bc	0.6 ± 0.5bc	1.1 ± 0.7bcd	0.1 ± 0.1c	0a
Oenothera biennis	1.2 ± 0.5bc	1.2 ± 0.7bc	1.4 ± 1.1bcd	0c	0a
Onopordum acanthium	0c	0c	0.1 ± 0.2cd	0.1 ± 0.1c	0a
Tragopogon dubius	1.5 ± 3.0bc	3.0 ± 2.6b	2.5 ± 3.0bcd	6.0 ± 4.3ab	0a
Tragopogon pratensis	1.5 ± 1.9bc	1.5 ± 1.9bc	0d	2.5 ± 1.9abc	0a
Verbascum blattaria	0c	0c	0d	0c	0a
Verbascum thapsus	0c	0.1 ± 0.1c	0.2 ± 0.2cd	0c	0a

Table 6.6. Comparison of the mean percentage (± S.D.) of seedlings of each of 15 biennial taxa which established within each of 5 gap sizes. Values for each taxa are expressed as a percentage of the number of seeds initially sown. Entries within a column followed by the same letter are not significantly different (P>0.05).

Species	40x40cm	30x30cm	20x20cm	10x10cm	No Gap
Alliaria petiolata	0c	0c	0c	0b	0b
Arctium minus	16.0 ± 3.5a	13.0 ± 10.9a	6.6 ± 4.8ab	4.6 ± 6.7ab	9.6 ± 8.9a
Cirsium vulgare	3.6 ± 3.6bc	3.4 ± 3.6abc	2.6 ± 3.0bc	0.2 ± 0.3b	0.9 ± 0.8b
Daucus carota	6.6 ± 6.9ab	5.1 ± 4.8abc	5.8 ± 9.0abc	1.7 ± 1.4b	0.4 ± 0.1b
Dipsacus sylvestris	9.2 ± 8.3ab	5.4 ± 1.3ab	2.9 ± 2.8bc	1.0 ± 2.0b	0.8 ± 1.1b
Echium vulgare	0.8 ± 0.5bc	0.9 ± 1.4bc	1.5 ± 2.7bc	0.5 ± 0.6b	0.8 ± 0.7b
Lactuca scariola	0c	0.2 ± 0.5bc	0.2 ± 0.5c	0b	0b
Melilotus spp.	1.0 ± 1.0bc	0.4 ± 0.4bc	0.4 ± 0.8c	0.6 ± 0.8b	0.2 ± 0.1b
Oenothera biennis	0.4 ± 0.4bc	0.1 ± 0.2bc	0.6 ± 0.8bc	0b	0b
Onopordum acanthium	0c	0c	0.1 ± 0.1c	0b	0b
Tragopogon dubius	4.0 ± 1.6abc	3.5 ± 2.5abc	3.5 ± 3.0bc	2.0 ± 2.3b	0b
Tragopogon pratensis	11.5 ± [illegible].5ab	14.5 ± 12.7a	14.5 ± 4.7a	12.0 ± 8.2a	7.5 ± 6.2a
Verbascum blattaria	0c	0c	0c	0b	0b
Verbascum thapsus	0c	0c	0c	0b	0b

seedlings than any other species. Of the remaining species, only *Daucus carota* and *Tragopogon dubius* had a mean percentage establishment which was significantly ($P<0.05$) greater than 0. Three species, *Cirsium vulgare*, *Onopordum acanthium*, and *Verbascum blattaria*, had no seedlings establish in this treatment. In the 1:1 treatment *Echium vulgare* had a significantly ($P<0.05$) greater percentage of established seedlings than any species except for *Daucus carota*. The only species which had no seedlings establish in this treatment were *Tragopogon pratensis* and *Verbascum blattaria*. In the 1:3 treatment *Echium vulgare*, *Lactuca scariola*, and *Tragopogon dubius* had mean percentages of established seedlings which were significantly ($P<0.05$) greater than 0. Three species, *Oenothera biennis*, *Verbascum blattaria*, and *Verbascum thapsus*, had no seedlings establish in this treatment.

For six taxa in this experiment, there were statistically significant ($P<0.05$), if not dramatic, differences between treatments in the percent of seeds sown which produced established seedlings. *Arctium minus* and *Echium vulgare* had no differences between treatments where seedlings were present, but the 100% gravel treatment where no seedlings established was significantly lower (Appendix 1). *Oenothera biennis* had no difference between treatments where seedlings were present, but the 1:3 and 100% gravel treatments where no seedlings established were significantly lower ($P<0.05$) (Appendix 1). In both *Daucus carota* and *Melilotus* spp. the percentage of established seedlings in the 1:1 treatment was significantly larger than that in the 1:3, but the 1:1 and 3:1 treatments were not different from 1:3 (Appendix 1). In contrast, the percentage of *Lactuca scariola* seedlings which

established was greater in the 1:3 treatment than in 100% sand or 3:1 although 1:1 was not different from any other treatment (Appendix 1). *Verbascum blattaria* failed to establish in any treatment (Appendix 1). For the remaining species there were no statistical differences ($P>0.05$) in the percent of seedlings which established between treatments whether or not any seedlings were present (Appendix 1).

Among the taxa not specifically mentioned in the preceding paragraph there were no statistically significant differences in mean percent seedling establishment ($P>0.05$) between treatments. Six of them had tendencies however, which might be of importance in determining their pattern of distribution in the field. *Dipsacus sylvestris* had no apparent pattern in its response to the treatments (Appendix 1). *Verbascum thapsus*, *Cirsium vulgare*, and *Onopordum acanthium* had small sporadic establishment, yet there was a tendency for seedlings of *Verbascum thapsus* to establish in the finer to medium textures, whereas those of *Onopordum acanthium* and *Cirsium vulgare* established in medium to coarser textures (Appendix 1). Seedlings of the remaining 3 species, *Alliaria petiolata*, *Tragopogon dubius* and *Tragopogon pratensis*, were able to establish across the range of treatments, but all had a marked tendency to establish in greater numbers in the 1:3 treatment (Appendix 1).

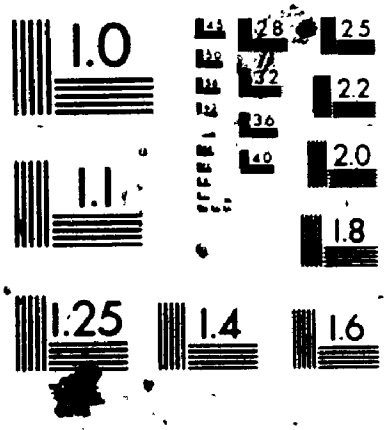
2. Gap size experiment

A comparison of the percentage of seeds of each species which were present as established seedlings within each treatment in the gap size experiment are presented in Table 6.6. Seedlings from the largest variety of species (11) were able to establish in the 20 x 20cm gaps. In the 40 x 40cm gaps *Arctium minus*, *Daucus carota*, *Dipsacus sylvestris*, and *Tragopogon pratensis* each had a mean percentage seedling establishment which was significantly ($P<0.05$) greater than 0. Four species, *Lactuca scariola*, *Onopordum acanthium*, *Verbascum blattaria*, and *Verbascum thapsus*, had no seedlings establish in this treatment. In the 30 x 30cm gaps three species, *Arctium minus*, *Dipsacus sylvestris*, and *Tragopogon pratensis* each had a percentage of established seedlings which was significantly ($P<0.05$) greater than 0. *Alliaria petiolata*, *Onopordum acanthium*, *Verbascum blattaria*, and *Verbascum thapsus* had no seedlings establish in this treatment. In the 20 x 20cm gaps only *Arctium minus* and *Tragopogon pratensis* had mean percentage seedling establishment which was significantly ($P<0.05$) greater than 0. Three species, *Alliaria petiolata*, *Verbascum blattaria*, and *Verbascum thapsus*, had no seedlings establish in this treatment. In the 10 x 10cm gaps only *Tragopogon pratensis* had a percentage of established seedlings which was significantly ($P<0.05$) greater than 0. Six species, *Alliaria petiolata*, *Lactuca scariola*, *Oenothera biennis*, *Onopordum acanthium*, *Verbascum blattaria*, and *Verbascum thapsus*, had no seedlings establish in this treatment. In the no gap treatment both *Arctium minus* and *Tragopogon pratensis* had a significantly greater ($P>0.05$) percentage of established seedlings than any other species. Seven species,

Alliaria petiolata, *Lactuca scariola*, *Oenothera biennis*, *Onopordum acanthium*, *Tragopogon dubius*, *Verbascum blattaria*, and *Verbascum thapsus* had no seedlings establish in this treatment.

In the gap sizes used in this experiment there were statistically significant (P>0.05) differences between treatments in the percent of seeds sown which were present as established seedlings in one species only. For *Dipsacus sylvestris* the percent of established seedlings was significantly greater in the 40x40cm gap than in the 10x10cm gap (Appendix 2). The percentages present in the 30x30cm and 20x20cm gaps however were neither different from one another nor from that of any other treatment (Appendix 2). *Alliaria petiolata*, *Verbascum blattaria*, and *Verbascum thapsus* failed to establish in any treatment, and for the remaining species there were no statistically significant (P>0.05) differences between treatments, whether or not any seedling established (Appendix 2).

Among the taxa not specifically mentioned in the preceding paragraph there were no statistically significant differences (P>0.05) between treatments in the mean percentage of seedlings which established. Nine of them had tendencies however, which might be of importance in determining their pattern of distribution in the field. *Tragopogon pratensis* had no apparent pattern in its response to the treatments (Appendix 2). *Echium vulgare*, *Lactuca scariola*, *Melilotus spp.*, *Oenothera biennis*, and *Onopordum acanthium* had low, sporadic establishment, yet there was a tendency for seedlings of *Melilotus spp.* to establish in greater numbers in the largest gap (Appendix 2), those of *Oenothera biennis* to establish in the 3 largest gaps (Appendix 2), and for those of *Echium vulgare*, *Lactuca scariola*, and



Onopordum acanthium to establish in greater numbers in the medium-sized gaps (Appendix 2). The remaining three species, *Cirsium vulgare*, *Daucus carota*, and *Tragopogon dubius* were able to establish across a range of treatments, but each had a marked tendency to establish to a in greater numbers in the 3 largest gaps (Appendix 2). *Arctium minus* had a curious tendency to establish in greater numbers in the 2 largest gaps as well as the no gap treatment (Appendix 2). Possibly, the small numbers of seedlings of this species which established in the 10x10cm gap treatment were the result of intraspecific density dependent mortality brought on by the flush of emergence which occurred in July, a time of low moisture availability in the field.

E. Flowering

Over the course of both the soil texture and the gap size experiments a few individuals of some species of biennials bolted and flowered. In the soil texture experiment the numbers of individuals which flowered were: *Tragopogon dubius* 22, *Tragopogon pratensis* 10, *Daucus carota* 2, *Echium vulgare* 2, and *Lactuca scariola* 17. In the gap size experiment the numbers of individuals which flowered were: *Tragopogon dubius* 26, *Tragopogon pratensis* 64, and *Melilotus officinalis* 1.

6.4 Discussion

A. Soil texture experiment

In nature, soil heterogeneity affects germination largely through moisture relations with the seed (Sheldon 1974, Pareja and Staniforth 1985, Fenner 1985). The germination of a surface-sown seed is a perilous process. Given a favorable temperature regime the seed must absorb water from the substrate faster than it loses water through evaporation to the atmosphere in order to imbibe sufficiently to germinate. This process is often difficult for a large seed because of its large surface area/soil contact area ratio. At the same time it encounters rapid, extreme fluctuations in temperature, moisture and humidity both daily and seasonally as well as pathogens and predators (Harper et al. 1970, Dowling et al. 1971, Sheldon 1974, Oomes and Elberse 1976, Harper 1977, Fenner 1985). Burial of the seed will decrease the area from which water can be lost to evaporation, but burial can also reduce gaseous exchange and thereby induce dormancy (Wesson and Wareing 1969b, Sheldon 1974, Fenner 1985). Seeds which remain on the surface and are able to acquire sufficient water to germinate face the barrier of the soil surface (Campbell and Swain 1973). Upon germination a radicle must penetrate the soil surface quickly in order to avoid death from desiccation (Campbell and Swain 1973, Sheldon 1974). To penetrate the soil surface a radicle must exert more pressure on the surface than the resistance of the surface (Campbell and Swain 1973, Sheldon 1974). To achieve maximum pressure, the root must anchor, normally through the action of the root hairs (Campbell and Swain 1973, Sheldon 1974). Often seedlings with

thick radicles have difficulty exerting sufficient pressure to penetrate the soil (Campbell and Swain 1973, Dowling et al. 1961). Even seedlings with slim radicles can have difficulty in anchoring on a smooth compact surface (Sheldon 1974) or a highly mobile, unconsolidated surface such as sand (Zedler et al. 1983). For optimal germination the seed needs to come to rest in a soil with an aggregate size which provides aeration and moisture to the germinating seed and subsequent radicle of the seedling (Pareja and Staniforth 1985).

The 100% gravel treatment provided the greatest degree of surface heterogeneity present in this experiment. Macropores were numerous and extended 0.3m deep to the soil underlying this treatment. While adequate aeration existed for all seeds sown into this treatment, moisture was undoubtedly in short supply for any seeds which lodged on a stone, and for seeds which fell through the stones the depth of burial was probably too great for successful emergence (*e.g.*: *Melilotus* spp.) or the lack of light induced dormancy (*e.g.*: *Verbascum thapsus*, *Verbascum blattaria*). A few individuals from 5 species (Figure 6.8) were present during the November sampling period. No seedling survived the winter, after contending with desiccation, subfreezing temperatures and frost-heaving, and none was present in this treatment in June or during any subsequent sampling period (Figure 6.8).

The 1:3 treatment provided heterogeneity of surface as well as a matrix of sand. The sand limited the depth of the macropores, created improved water retention, and provided a medium in which seedlings could root. In this treatment seeds could lodge on a water supplying surface below the

soil surface in well aerated macropores shielded from the high evaporation of the surface. The largest number of seedlings present in November for any treatment were present under these relatively favorable germination conditions (Figure 6.2). Factors which favor germination, however, do not always favor establishment (Sheldon 1974). There were one third fewer seedlings present in this treatment in June than in November (Figure 6.2), a number which included the emergence of those species not present in the fall (Figure 6.7). Most probably settling of the sand and frost-heaving over winter accounted for the seedling deaths. Many studies have demonstrated that, within a species, seedlings which germinate early and pre-empt resources from their competitors are larger and more successful than later germinators (Ross and Harper 1972, Baskin and Baskin 1972, Arthur et al. 1973, Hawthorn and Cavers 1976, Symonides 1977, Weaver and Cavers 1979, Cook 1980, Gross 1980b, Howell 1981). In this treatment many of the seedlings of *Echium vulgare* which emerged in the fall successfully overwintered. In spring they rapidly expanded their size advantage to the point where all four replicates in this treatment had a canopy of *Echium vulgare* foliage which provided ≥75.0% cover. Prince and Marks (1982) found that buried seeds of *Lactuca scariola* could be vernalized. A sizable majority of the individuals of this species which emerged in the 3:1 treatment bolted and flowered, so apparently the conditions present in this treatment were suitable for vernalization of seeds of *Lactuca scariola*.

The 100% sand treatment presented a soil surface which was unconsolidated, mobile, and devoid of features which would aid a seed in lodging or burial. Sand has little capacity to hold water and the top few

centimeters can dry up very quickly after a summer rain (de Jong and Klinkhammer 1986). In the replicates of this treatment virtually no seedlings emerged where the seeds had originally been sown; rather emergence occurred along the inside edges of the plywood forms which held the treatments. This pattern of emergence indicated that seeds were moved from their original place of deposition to an area where they were able to germinate and anchor. Presumably once they had been washed or blown to the edges of the form, they were partially buried by sand and this burial facilitated germination and emergence (Zedler et al. 1983). The numbers of seedlings present in this treatment were consistently lower than those present in either the 3:1 or the 1:1 treatments and the number of seedlings which ultimately established was very similar to the total established in the 1:3 treatment (Figure 6.2). Presumably the low numbers of seedlings which emerged in this treatment resulted from poor moisture relations, and the relatively small numbers of seedlings which were present in July and the low numbers that established were the result of the late summer drought drying the sand to a depth below the level of the roots of the seedlings.

Small-seeded species such as *Oenothera biennis*, *Verbascum blattaria* and *Verbascum thapsus* were readily able to incorporate into the uppermost level of sand and they emerged well in this treatment (Figure 6.4). The most abundant taxa during all sampling periods in this treatment however, were those which had relatively drought-tolerant seedlings (Figure 6.4). Three of these, *Melilotus alba*, *Melilotus officinalis*, and *Daucus carota*, are the most numerous biennial species in the study area (Table 2.2).

The remaining two treatments, 75% sand to 25% gravel and 50% sand to 50% gravel, presented the same sort of surface texture to a colonizing seed; the only difference was in degree. In each treatment there were surface features which would facilitate a seed lodging and becoming buried, and a sand medium in which the seedling could root. There was not much difference in the species composition or numbers of individuals which were present in these treatments in either November or June (Figures 6.2 and 6.6). In both treatments *Echium vulgare* had the greatest numbers of seedlings present throughout the summer, whereas *Daucus carota* was numerous in November. In the 3:1 treatment small-seeded species, *Verbascum thapsus*, *Verbascum blattaria*, and *Oenothera biennis* were more numerous than in the 1:1 treatment, possibly because in the finer texture they tended not to get buried as frequently to a depth that induced dormancy (Figure 6.5). In contrast, the *Melilotus* spp. were more numerous in the 1:1 treatment, possibly because the greater surface heterogeneity facilitated burial of their seeds, improved their water relations, and provided channels for the relatively thick radicles of their seedlings to follow in penetrating the soil (Figure 6.6). Although the numbers of seedlings present in both these treatments were very similar in June, numbers present in the 1:1 treatment remained higher in July and September (Figure 6.2). This is probably because the greater stone content of the 1:1 treatment improved its soil water holding capacity. Water tends to drain through sand rapidly and dry it out. The gravel particles which were present in the sand in this treatment, however, served as water collection points, and to a small extent water could pool on the upper surfaces of buried stones.

From the results of the soil texture experiment (Figures 6.4 through 6.8; Tables 6.5 and Appendix 1), it is clear that differences between these biennial species in emergence and establishment will occur in the Marshall pit, and that such differences will result from the texture of the substrate which their seeds encounter. None of the species under study would be expected to be present in 0.3m deep gravel since no seedlings could establish there (Table 6.5). In areas of finer to medium texture, *Arctium minus*, *Daucus carota*, *Melilotus* spp., *Oenothera biennis*, *Echium vulgare* and *Verbascum thapsus* would be expected to establish in larger numbers, whereas in areas of medium to coarse texture *Echium vulgare*, *Alliaria petiolata*, *Cirsium vulgare*, *Lactuca scariola*, *Onopordum acanthium*, *Tragopogon dubius* and *Tragopogon pratensis* would be expected to establish in greater numbers and this is, in fact, what happens (Appendix 1). The greater presence of *Cirsium vulgare*, *Tragopogon pratensis*, *Tragopogon dubius* and *Lactuca scariola* in the 1:3 treatment could be an artifact of the method of seed pretreatment. It is possible that this treatment simply was the one which allowed these achenes to enter a fissure and lodge at a proper orientation to achieve maximum water uptake. Possibly if the pappus had been left attached, seeds of these species would have been able to germinate in larger numbers in the other treatments.

B. Gap size experiment

In closed vegetation seedlings are often unable to acquire enough resources to compete with established vegetation. An opening in the vegetation is a place of reduced competition for resources, particularly light

and water (at least with regard to established plants), different light quality, greater insolation, and greater fluctuations in temperature and moisture (Evans and Young 1972, Cook 1979, Fenner 1985). The environmental conditions prevalent within a gap are so different from those in the surrounding vegetation that many species, particularly ruderals which depend on gaps for their successful regeneration, have 'gap detection' mechanisms through which seed germination is stimulated when a gap is 'located' (Fenner 1985). Among these mechanisms are the requirement for fluctuating temperatures to break dormancy (Thompson and Grime 1983) and the inhibition of germination by light transmitted through a leaf canopy (King 1975, Gorski et al. 1977, Silvertown 1980). Many of the properties of a gap such as amount of insolation, the magnitude of temperature fluctuation, and degree of moisture availability are highly correlated with its size (Fenner 1985). Larger gaps have greater temperature and moisture fluctuations and more light available than small gaps (Evans and Young 1972, Goldberg and Werner 1983, Fenner 1985). Work by Goldberg and Werner (1983) has indicated that different species require different minimum sized openings for establishment. Yet, even within a single gap, conditions are often variable enough to allow the establishment of several species (Fenner 1985). Both Miles (1974) and Davis and Cantlon (1969), using artificially created gaps of similar size to the ones used in this study found that some species established at the center of the gap while others established at its edges.

Colonizing seedlings faced the greatest competition from existing vegetation in the no gap treatment. On all sampling dates the number of seedlings present in this treatment was consistently lower than the number

present in any other treatment (Figure 6.3). The presence of vegetation and litter suppressed germination of all but two species in the first fall and competition with established vegetation resulted in death for all but one *Tragopogon pratensis* seedling by the November sampling period (Figure 6.13). By June, the activities of small mammals had created some small openings in this treatment and individuals from several species began to exploit them (Figure 6.13). By July, the numbers of individuals in this treatment peaked, but then the late summer drought came and the numbers of seedlings present were undoubtedly reduced by competition for moisture with the surrounding vegetation. The reason that the decline in seedling numbers in the no gap treatment was not as dramatic as that in the 10x10cm gap treatment was that those of *Arctium minus* (the most numerous species in the no gap treatment) apparently had great tolerance for competition, whereas in the 10x10cm gap the most numerous species, *Dipsacus sylvestris*, apparently a poor competitor, incurred most of the seedling mortality (Figures 6.12 and 6.13).

Because of the results of the gap size experiment, I believe that very little segregation would occur between these biennial species in the Marshall pit as a result of the differential utilization by their seedlings of foliar gaps of the dimensions provided as treatments in this experiment. *Alliaria petiolata*, *Verbascum blattaria*, and *Verbascum thapsus* would be expected to be very rare or absent in standing vegetation or smaller gaps, but seedlings of the remaining species could potentially be present in gaps ranging in size from 10x10cm to 40x40cm. Seedlings of most of these species, except for *Tragopogon pratensis*, would be present in greater numbers in

the larger gaps (Table 6.6).

C. Individual species performance

Gross and Werner (1982) and Gross (1984) demonstrated that for 6 biennial species which occurred in old fields in southern Michigan, seed size was the principle factor which determined the types of microsites they could colonize. The response of the biennial species in my study to the treatments provided in both the soil texture and the gap size experiments however, was not merely a function of their relative seed sizes, but was rather the product of their individual germination responses and their seed and seedling characteristics. My findings are in accordance with those of Harper and Clatworthy (1963) who investigated two *Trifolium* species of greatly differing seed weights. They found that the initial disadvantage of small seed size could be ameliorated by subsequent seedling behavior. An investigation of these characteristics for each of my biennials, as is done in the following sections, should reveal many of the underlying reasons for their behavior both in the soil texture and gap size experiments and in the study area.

The size of the embryo and its resultant seedling are more critical to the process of establishment than is the size of the seed (Fenner 1983, Fenner 1985). Even though there is evidence that the embryo is proportionally smaller in large seeds than it is in smaller seeds, in terms of absolute seedling size, many studies both within and between species have shown that seed size is directly correlated with seedling size, larger seeds produce larger seedlings (Salisbury 1942, Black 1958, Harper and Clatworthy 1963,

Cavers and Harper 1966, Harper et al.. 1970, Baker 1972, Weis 1982, Gross and Werner 1982, Fenner 1983, Gross 1984, Stanton 1984, Stanton 1985, Wulff 1986b). After germination the growth of the emergent seedling is largely dependent on its internal food reserves until the expansion of its root and shoot systems allow it to be sustained by its own photosynthesis (Fenner 1985). A large seed then, which provides a substantial food reserve produces a seedling which can rapidly achieve what may prove to be a critical size for survival. This will put it on a competitive footing with other plants. Consequently, possession of a large seed is generally assumed to be of advantage (Salisbury 1942, Harper 1977, Gross 1984, Fenner 1985). Seed size in a plant species however, represents a compromise between the demands of dispersal and establishment (Harper et al. 1970, Salisbury 1942, Fenner 1985). Generally speaking, species which exploit widely scattered open sites where competition is either minimal or absent have small, highly dispersable seeds which may form persistent seed banks, have extreme longevity in the soil and have various gap and depth detecting mechanisms associated with their germination, whereas species which inhabit more stable closed environments tend to have larger seeds which form briefly persistent or transient seed banks, have little longevity in the soil, and germinate readily (Salisbury 1942, Harper 1977, Grime 1979, Silvertown 1982, Fenner 1985). In addition to closed communities, species with large seeds are also associated with dry habitats where rapid development of a root system is essential for seedling survival (Salisbury 1942, Cavers and Harper 1966, Cavers and Harper 1967b, Baker 1972, Weis 1982, Wulff 1986b).

Gross and Werner (1982) and Gross (1984) investigated the emergence and establishment of six biennial species differing in seed weights in a variety of cover types both in an old field environment and under controlled conditions in a greenhouse. They found that while emergence of all species was not necessarily related to cover, small seeded species failed to establish except in bare patches, that large seeded species had a slower relative growth rate and a greater final seedling size when grown in competition with standing vegetation, and that in the absence of competition from vegetation, initial seed weight is independent of final seedling size (Gross and Werner 1982, Gross 1984). The biennials in the current study were divided into large, intermediate, and small size classes following the convention of Gross (1984) (see 3.2 C.). The response of these biennials to the treatments in the gap size and soil texture experiments were variable within each size class.

The species in the large size class were *Arctium minus*, *Onopordum acanthium*, *Tragopogon dubius*, and *Tragopogon pratensis*. *Onopordum acanthium* forms a large persistent seed bank made up of long-lived seeds (4.4 C.). Very few seedlings of this species were present in either experiment, because of low germination resulting from the presence of a water soluble inhibitor and a high temperature requirement for germination (4.4 B.).

Seeds of *Tragopogon pratensis* and *Tragopogon dubius* are shed in mid-summer (2.2), undergo a period of afterripening at high temperatures (4.4 B.) and their seedlings emerge in late summer (2.2). Neither species forms a persistent seed bank. Many biennial species must achieve a critical minimum size before they can become vernalized to flower the following year (Werner

1975b, Baskin and Baskin 1979a, Baskin and Baskin 1979b, van der Meiden and van der Waals-Kooi 1979, Grosk 1981, Gross and Werner 1983, de Jong and Klinkhammer 1986). Most seedlings of both *Tragopogon pratensis* and *Tragopogon dubius* which emerged in the fall were able to reach this critical size, and these flowered in the next year. Seedlings of both species established in equivalent numbers in the finer textured treatments and the two largest gap sizes (Tables 6.5 and 6.6), but *Tragopogon pratensis* established in significantly larger ($P<0.05$) numbers in the smallest gap and the no gap treatments (Table 6.6). This result is in accordance with Harper et al. (1970) who noted that among congeneric species having different seed sizes, the larger seeded species is often found in the more closed habitats.

Although seeds of *Arctium minus* are capable of fall germination (4.4 B.), few encounter sufficiently favorable conditions to do so. Most seeds overwinter before emerging the following spring (4.4 B.). In the gap size experiment there was a second flush of emergence in July perhaps associated with the clipping of the background lawn. Seeds of this species emerged in greater numbers in the gap size experiment than in the soil texture experiment, except for the 1:3 treatment, possibly because the large seeds had difficulty both in becoming buried and acquiring sufficient water to germinate. In the 1:3 treatment, where adequate fissures were present in the soil surface to allow seed burial, emergence was as great as it was in the gap size treatments. Fewer seedlings established in the soil texture treatments than in the gap size treatments, indicating that perhaps this species is primarily adapted for regeneration in vegetation rather than in areas of drought stress.

The taxa with seeds of intermediate size, *Alliaria petiolata*, *Cirsium vulgare*, *Dipsacus sylvestris*, *Daucus carota*, *Echium vulgare*, *Lactuca scariola*, and *Melilotus* spp. also possess a variety of responses to the experimental treatments. Four of these taxa, *Alliaria petiolata*, *Echium vulgare*, and *Melilotus* spp., have innately dormant seeds and can form sizeable persistent seed banks (4.4 C.). *Alliaria petiolata* has physiologically deep-dormant seeds (4.4 B.) and its emergence after the first year of sowing in treatments of both experiments was unexpected. Low and sporadic emergence in the gap size treatments indicate that conditions were unfavorable for stimulation of germination and subsequent failure to establish indicates that seedlings are probably not good competitors. In contrast, the establishment of *Alliaria petiolata* seedlings in all treatments in the soil texture experiment indicates that seedlings of this species tolerate drought relatively well.

The nature of the dormancy present in seeds of *Echium vulgare* is uncertain (4.4 B.), but the conditions prevalent in the soil texture treatments seemed to promote germination to a greater degree than those in the gap size treatment. Seedlings emerged in every treatment of both experiments and established in every treatment except 100% gravel. Much higher percentages of seedlings of this species emerged and established in the nutrient poor, dry, soil texture treatments than did in the contrasting conditions of the gap size treatments. These findings are in accordance with those of Klemow and Raynal (1985) who reported that seedlings of *Echium vulgare* were particularly drought tolerant and that the demography of this species was largely unaffected by site conditions found in an abandoned

limestone quarry. The only clear-cut example of early seedling emergence pre-empting biological space (*sensu* Ross and Harper 1972) occurred with *Echium vulgare* in the 1:3 treatment in the soil texture experiment. Seedlings which emerged in the fall gained enough advantage to overgrow the treatment before the July sampling period.

Both *Melilotus alba* and *Melilotus officinalis* have innately dormant seeds and form persistent seed banks (4.4 C.). Dormancy in these species is the result of a seed coat impermeable to water which leads to delayed germination (4.4 B.). Seeds of these species emerged in all treatments in both experiments and established to some extent in every treatment except the 100% gravel. Their low percentage of emergent seedlings results from a combination of hard seeds becoming incorporated into the seed bank and pre-emergence seed mortality (5.3 B.). The greater percentage emergence of these species in the two largest gap sizes is the result of a gap and depth sensing mechanism inherent in the seed. Under field conditions, the strophiole increases in permeability to water as a response to the diurnal temperature fluctuations it encounters in the soil (4.4 B.). The magnitude of such fluctuations become more extreme with increasing gap size (Grime et al. 1981). Caruso (1970) also found that while gap size had no correlation with emergence, more seedlings of both *Melilotus alba* and *Melilotus officinalis* survived in larger gaps.

The remaining 4 species with intermediate sized seeds do not form large persistent seed banks. One of them, *Daucus carota*, has a large proportion of seeds which are innately dormant when freshly matured (4.4 B.). A chilling requirement which must be met before germination can occur is not

uncommon among seeds of species in the Umbelliferae (Grime et al. 1981); it times emergence to occur in the most favorable season. Seedlings of *Daucus carota* emerged in all treatments in both experiments and established to some extent in all treatments except 100% gravel. These findings are in accordance with those of Gross and Werner (1982) and Gross (1984) who found that seedlings of *Daucus carota* emerged and established in both bare ground and vegetated cover.

Lactuca scariola, *Cirsium vulgare*, and *Dipsacus sylvestris* neither form persistent seed banks nor have innately dormant seeds (4.4 B.). If dispersed seeds of one of these species fail to encounter favorable conditions for germination however, they are induced into dormancy until the following spring (4.4 B.). *Lactuca scariola* generally had low and sporadic emergence in these two experiments. The exception is in the 1:3 treatment of the soil texture experiment; but as previously discussed, the sizeable percent emergence in this treatment as contrasted with the low percent emergence in all other treatments is in all likelihood an artifact of the seed pretreatment. Seedlings of *Lactuca scariola* were able to establish in small numbers in intermediate treatments in both experiments. Prince and Marks (1982) found that buried seeds of this species could become vernalized so that flowering could take place the following year. Conditions in the soil texture treatments apparently were favorable for seed vernalization as virtually all *Lactuca scariola* seedlings which emerged in this experiment flowered.

Seedlings of *Cirsium vulgare* emerged in very low numbers in the soil texture experiment and established in low numbers in the only two

treatments in which they had emerged. This low percent emergence is possibly the result of high levels of pre-emergence mortality (5.4 B.), but van Leeuwen (1981) found that the activities of soil microflora on the seed coat inhibited germination of *Cirsium vulgare* in nutrient-poor sites. Perhaps the low percentage emergence of this species in the soil texure experiment is the result of microbial activity. In the gap size experiment seedlings emerged and became established in all treatments, again possibly as a result of microbial action. Van Leeuwen (1981) found that in nutrient-rich areas the activities of soil microflora on the seed coat promoted germination in this species. These responses indicate that *Cirsium vulgare* seedlings do not tolerate drought well and are better adapted to establishment in open vegetation.

Seedlings of *Dipsacus sylvestris* were able to emerge and establish in every treatment in the soil texture experiment except for 100% gravel. The small number of seedlings which emerged in this experiment is probably the result of pre-emergence mortality (5.4 B.), and the small proportion of emerged seedlings which established undoubtedly reflects low drought tolerance in seedlings of this species (5.4 D.). In the gap size experiment, seedlings of *Dipsacus sylvestris* emerged in large numbers in the three larger gaps and in lesser numbers in the smallest gap and the no gap treatments. The small number of established seedlings in each treatment reflected a loss of emerged individuals, and the proportion lost increased with decreasing gap size. This response is in accordance with the work of Werner (1977), Werner and Gross (1982), and Gross (1984) who found that while seedlings of *Dipsacus sylvestris* could emerge and survive in both

bare ground, and under vegetative cover, survival and growth of seedlings of this species were greater in bare ground (5.4 B. and 5.4 D.).

The three small-seeded species, *Oenothera biennis*, *Verbascum blattaria*, and *Verbascum thapsus* are similar in that their seeds have no innate dormancy, but can be induced into a deep dormancy by burial or by exposure to light filtered through a foliar canopy. Once dormant, seeds of these species have extreme longevity in the soil (4.4 D.). They differ however, in the growth forms of their seedlings and in their response to light (Gross and Werner 1982, Gross 1984). Both *Verbascum blattaria* and *Verbascum thapsus* emerged sporadically and in very small numbers in the gap size experiment. No seedling of either species survived to establish in any treatment in this experiment. Gross and Werner (1982) and Gross (1984) also found that the small seedlings of *Verbascum thapsus*, being poor competitors in vegetated cover, required bare ground in which to establish. Seeds of both species emerged in all treatments in the soil texture experiment except for 100% gravel. No seedlings of *Verbascum blattaria* established in any treatment in this experiment, whereas those of *Verbascum thapsus* established in the medium-fine treatments. Apparently seedlings of *Verbascum blattaria* are intolerant of drought as well as shading, whereas some seedlings of *Verbascum thapsus* are drought tolerant. The low percent emergence of both species in the gap size and soil texture experiments is probably the result of seeds failing to have their dormancy broken by the conditions prevalent in the experimental treatments.

In contrast to *Verbascum blattaria* and *Verbascum thapsus*, the seedling of *Oenothera biennis* has an extremely vigorous radicle which

expands rapidly upon emergence to produce a relatively extensive root system. This large root presumably confers some measure of drought tolerance on the seedling. Seedlings of this species emerged in all treatments in the gap size experiment and in all treatments except the 100% gravel in the soil texture experiment. In the soil texture experiment seedlings established in the three finer textures. Seeds which failed to germinate probably were present but dormant (4.4 C.). Gross and Werner (1982) and Gross (1984) found that seedlings of *Oenothera biennis* were poor competitors in vegetative cover and were able to establish only on bare ground. The response of *Oenothera biennis* in the gap size experiment is in accordance with the findings of Gross and Werner (1982) and Gross (1984), and further suggests that a gap size greater than 100cm^2 is required for the establishment of seedlings of this species. Again, the low percent of seedling emergence in these treatments is the result of dormant seeds failing to germinate.

D. Comparison of the soil texture and gap size experiments

A direct statistical comparison of the responses of the biennial species to the soil texture and gap size treatments is inappropriate because of the differences in the experimental conditions. The substrate in the soil texture treatments was coarse, dry, and nutrient-poor in each case. The substrate in all treatments of the gap size experiment was a nutrient-rich loam with a finer texture and better water holding capacity. The presence of surrounding vegetation ameliorated the harshness of the microclimate. Despite competition from the standing vegetation, the gap size treatments

were on the whole more favorable for plant germination and growth (Cook 1979). Forty percent more seedlings established in the gap size treatments than in the soil texture treatments. The seedlings present in each experiment did not simply reflect the relative proportions of seeds of each species which were input into each treatment. Both within- and between- experiment differences in seedling response were apparent in this study.

In the gap size experiment the taxa with the largest number of seedlings established were those best adapted for competition with other seedlings and with established vegetation. In the soil texture experiment the taxa with the largest number of established seedlings were those best adapted for drought tolerance. Among the former taxa, *Arctium minus*, *Daucus carota*, and *Dipsacus sylvestris* (Table 6.3), only *Daucus carota* was numerous in the Marshall pit (Table 2.2). *Arctium minus* inourred heavy losses from its seed crop each year to a predator and so had insufficient propagules to exploit its potential safe sites. *Dipsacus sylvestris* has only localized dispersal and was categorized by Gross and Werner (1982) as a later successional species. Perhaps it had only recently colonized the Marshall pit at the time of this study and was in the process of expanding its population. Among the latter taxa, *Daucus carota*, *Echium vulgare*, and *Melilotus* spp., only *Echium vulgare* did not occur frequently in the study area (Table 2.2). It is a strongly drought-tolerant species (Klemow and Raynal 1985), but has slow growth and localized dispersal (3.4). Perhaps *Echium vulgare* at the Marshall pit is, as Klemow and Raynal (1985) found in their abandoned limestone quarry, a relatively recent colonizer. Given the harsh dry conditions prevalent in the Marshall pit it, too, was probably in the

process of expanding its population. *Melilotus* spp. was the second most frequent taxon in the study area (Table 2.2). Seedlings of these species established in both a range of soil textures and a range of gap sizes, so given their large reproductive potential (Table 3.2) and their persistent seed bank (4.4 C.), these species should remain numerous in the Marshall pit until the vegetation closes completely. *Daucus carota* had the largest number of established seedlings of any species in either experiment (Tables 6.2 and 6.3). The ability to emerge and establish in a wide range of soil textures and gap sizes largely explains why *Daucus carota* was also the most frequently occurring species in the study area (Table 2.2). Gross and Werner (1982) reported that this species was a later successional species in old fields in southern Michigan, so *Daucus carota* should be a major component of the Marshall pit vegetation for years to come.

Chapter 7

Discussion

This discussion of the results of the preceding experiments is divided into two parts. The first is a specific examination of how my results answer the two questions which were presented in Chapter 1 as the underpinning for this research. The second is a general view of the occurrence of biennials in southwestern Ontario and presents a possible explanation to account for the great amount of variation in life history characteristics which are present among what is presumably such a tightly defined group.

7.1 Answering the questions

The first question stated in Chapter 1 was "what is the range of variability in tactics (*sensu* Harper 1977) employed among species which have a biennial life history strategy?"

A range of variation existed among the 15 biennial species in every life history characteristic that I investigated. *Tragopogon dubius* and *Tragopogon pratensis* flowered in late May and had begun to produce ripe seeds by mid-June whereas *Oenothera biennis* and *Dipsacus sylvestris* began to flower in mid-July and did not produce ripe seeds until mid-September (see section 2.2). The mean height of the flowering stalk ranged from 45.4cm for *Oenothera biennis* to 133.3cm for *Melilotus alba* (Table 3.1). The minimum in estimated mean net seed production was 119 seeds/plant for *Tragopogon dubius* whereas the maximum was 22,425 seeds/plant for *Verbascum thapsus* (Table 3.2). The mean weight per seed ranged from 0.07mg for *Verbascum*

thapsus to 13.03mg for *Onopordum acanthium* (Table 3.3). Diaspores of *Arctium minus* and *Daucus carota* had obvious morphological adaptations for external carriage by animals, whereas those of *Cirsium vulgare*, *Lactuca scariola*, *Tragopogon dubius*, and *Tragopogon pratensis* were obviously adapted for wind transport, and those of the remaining species had no obvious morphological adaptations for dispersal (see section 3.4 D.). Freshly ripened seeds of *Arctium minus*, *Cirsium vulgare*, *Dipsacus sylvestris*, *Lactuca scariola*, *Verbascum blattaria*, and *Verbascum thapsus* had no innate dormancy and were capable of immediate germination (Table 4.1, Figure 4.2 a-f); they could however, be rapidly induced into secondary dormancy (see section 4.4 B.). Seeds of both *Tragopogon dubius* and *Tragopogon pratensis* had a high temperature after-ripening requirement (see section 4.4 B. and Figure 4.2 g and h). A portion of the freshly ripened seeds of *Oenothera biennis* and *Daucus carota* were capable of immediate germination, but the majority of those of each species were innately dormant and required stratification to break their dormancy (Figure 4.2 i and j, see also section 4.4 B.). Both *Melilotus alba* and *Melilotus officinalis* had seeds whose innate dormancy was enforced by an impermeable seed coat (see section 4.4 B. and Figure 4.2 k and m). *Alliaria petiolata*, *Echium vulgare*, and *Onopordum acanthium* all had innately dormant seeds in which the dormancy was physiological in nature (see section 4.4 B. and Figure 4.2 l and n). *Daucus carota*, *Echium vulgare*, *Melilotus alba*, *Melilotus officinalis*, *Oenothera biennis*, *Onopordum acanthium*, and *Verbascum thapsus* all formed persistent seed banks in the study area (Figure 4.6). *Alliaria petiolata*, *Arctium minus*, *Cirsium vulgare*, and *Lactuca scariola* have been reported in other studies to form persistent seed banks and *Verbascum blattaria* undoubtedly does

so (see section 4.4 C.). Of the species in this study, only *Tragopogon dubius* and *Tragopogon pratensis* form transient seed banks (see section 4.4 C.). Longevities in the soil of the seeds of my biennials range from less than 1 year for both *Tragopogon dubius* and *Tragopogon pratensis* to at least 100 years for *Verbascum blatatria* and *Verbascum thapsus* (see section 4.4 D.). Seedlings of *Cirsium vulgare*, *Dipsacus sylvestris*, *Echium vulgare*, *Lactuca scariola*, *Onopordum acanthium*, *Oenothera biennis*, *Verbascum blattaria*, and *Verbascum thapsus* had their leaves oriented parallel to the ground surface, whereas those of *Alliaria petiolata*, *Arctium minus*, *Daucus carota*, *Melilotus alba*, *Melilotus officinalis*, *Tragopogon dubius*, and *Tragopogon pratensis* were oriented perpendioularly to the ground surface (Figure 5.1). There was a statistically nonsignificant tendency for greater numbers of seedlings of *Cirsium vulgare*, *Daucus carota*, *Tragopogon dubius*, and *Tragopogon pratensis* to emerge in densely vegetated plots than in sparsely vegetated plots, whereas significantly ($P<0.05$) greater numbers of seedlings of *Dipsacus sylvestris*, *Lactuca scariola*, and *Verbascum* spp. emerged in the sparsely vegetated plots (Table 5.1). The numbers of seedlings which emerged in the sparsely vegetated plots ranged from 0 for *Alliaria petiolata* to 394 for *Daucus carota* (Table 5.1). In the densely vegetated plots the numbers of seedlings which emerged ranged from 0 for *Alliaria petiolata* to 476 for *Daucus carota* (Table 5.1). Mean percent seedling establishment in the sparsely vegetated plots ranged from 0 in *Alliaria petiolata* and *Onopordum acanthium* to 82.7% in *Melilotus* spp.(Table 5.3). In the densely vegetated plots, mean percentage seedling establishment ranged from 0 for *Alliaria petiolata* and *Onopordum acanthium* to 91.7% for *Melilotus* spp. (Table 5.3). There was a statistically nonsignificant tendency for

seedlings of *Arctium minus*, *Daucus carota*, *Melilotus* spp., *Oenothera biennis*, and *Verbascum thapsus* to establish in greater numbers on fine to medium textured substrates, whereas there was a statistically nonsignificant tendency for those of *Alliaria petiolata*, *Cirsium vulgare*, *Lactuca scariola*, *Onopordum acanthium*, *Tragopogon dubius*, and *Tragopogon pratensis* to establish in greater numbers on the medium to coarse textured substrates (Figures 6.4-6.8, Table 6.5, Appendix I). Seedlings of *Echium vulgare* established equally well regardless of the soil texture (Figures 6.4-6.8, Table 6.5, Appendix I). Those of *Alliaria petiolata*, *Verbascum blattaria*, and *Verbascum thapsus* failed to establish in any size of gap which was provided in my investigation, whereas those of the remaining species established in the 10x10 through 40x40cm gaps (Figures 6.9-6.13, Table 6.6, Appendix II). Seedlings of *Tragopogon pratensis* established in every gap size equally, but there was a statistically nonsignificant tendency among those of the remaining species to establish in greater numbers in the three larger sized gaps (Figures 6.9-6.13, Table 6.6, Appendix II).

Taken in total the variation in regeneration characters present among my biennials does not represent the extremes of the range present among higher plants. For example, in dunes in Britain *Vulpia fasciculata* (Forskal) Samp. normally produces on average only 1.7 mature seeds/plant (Watkinson 1978) whereas *Orchis maculata* L. may produce from 750,000 to 1,000,000 seeds throughout the course of its life (Salisbury 1942). The double coconut palm (*Lodoicea maldivica*) may produce seeds whose weight ranges from 18 to 27kg whereas those of *Goodyera repens* (L.) R.Br. weight 0.000002g (Harper et al. 1970). Seeds of tropical rain forest trees have a longevity of mere

dormancy whereas seeds of the Indian water lotus (*Canna compacta*) have been reported to remain viable for 620 years (Fenner 1985). Further, because of the harsh environmental conditions in the Marshall pit, the full range of life history characteristics possible among my 15 biennial species was not reached in this study. For example, Turkington et al. (1978) reported that *Melilotus alba* could produce 350,000 seeds/plant when growing in isolation. I found a mean production of 9,712 seeds/plant for this species (Table 3.2). Werner (1975a) reported that the flowering stalk of *Dipsacus sylvestris* could range in height from 0.5 to 2.0m whereas I found the mean height of the flowering stalk of this species to be 1.23m (Table 3.1). Finally, Reinartz (1984b) reported that the seed bank of *Verbascum thapsus* had a density of 680 seeds /m² under pine stands in North Carolina, but I found a density of 2.6 seeds/m² for this species in the seed bank in July and 10.5 seeds/ m² in November. Clearly, while these 15 biennial species were variable in regeneration characteristics in the Marshall pit, they did not exhibit the full range of variation that was possible. In fact, in more favorable habitats they have the potential for even greater variability in the traits I investigated.

The second question posed in Chapter 1 was "are very similar species able to co-exist through differentiation in their regeneration characteristics?" The Marshall pit presented a habitat which was highly variable both in time and in space. Its substrate ranged from coarse gravel to coarse sand with large areas being a variable mixture of sand and gravel. Where vegetation had been present for several years there was some rudimentary soil development and, hence, a finer textured substrate was

present. The water-holding capacity of the substrate varied according to its texture. Where there was coarse texture, little water could be held. In contrast, areas of finer texture had reasonably good water-holding capacity. Levels of macronutrients were very patchy throughout the Marshall pit. Large areas were relatively poor in all nutrients. Localized areas, however, could be rich in one or more nutrients as the result of the build-up and decay of litter under standing vegetation, the actions of nitrogen-fixing bacteria, either free-living or associated with legumes such as *Melilotus alba*, *Melilotus officinalis*, or *Medicago lupulina*, or the decay of dung or the corpses of dead animals. At the time of my study, vegetation was also patchy in the Marshall pit. There were various sized islands with dense plant cover (more than 95%), bare areas (less than 5% plant cover), and large areas of sparse vegetation (from 10 to 75% plant cover).

The climate in the Marshall pit varies between years, across seasons within a single year, and within each day. Intensity of sunlight is less and daylength is shorter during late spring and early fall than they are in mid-summer. The climate of any given year is seldom identical to the 30 year normal in either temperature or precipitation (Figures 2.1 and 2.2). Within each year there is potential for heat waves, cold snaps, droughts and torrential rains. Mean monthly precipitation is particularly variable between years in the London, Ontario area (Figure 2.2). Within a single year temperatures range from those favorable for plant growth (April through October) to those lethal for growing plants (November through March) (Table 2.1). Much of the precipitation which falls during winter comes in the form

of snow (Table 2.2). An accumulation insulates the ground from bitterly cold temperatures and when it melts in spring there is briefly a superabundant supply of water flowing across the surface and draining through the substrate in the Marshall pit. Rain falls intermittently throughout the remaining months of the year, sometimes coming in brief violent deluges, sometimes in prolonged showers that may last for days.

The prevailing winds which pass through the Marshall pit change both in mean speed and in direction during the year (see 3.4 D.2.). However, the winds are also quite variable on the short-term basis. During a violent storm they might gust to 90km/hr whereas on calm days they may be gentle breezes which fail to register on a hand-held anemometer. Climate also varies diurnally. Every 24 hour period is sharply divided into day and night. During the day temperatures are higher and humidity is lower than during the night.

Substrate texture changes in the Marshall pit over time. Sand and gravel are moved by rain wash and snow melt and the surface is disturbed by frost-heaving and by the activities of animals (*eg*: burrowing by groundhogs).

The vegetation in the Marshall pit is also changing over time. Islands of dense perennial vegetation are expanding, bare patches of ground are colonized, and new bare patches are formed by the death of individuals. The presence of vegetation ameliorates an otherwise harsh environment. Decayed plant litter enriches the substrate, legumes fix nitrogen, soil horizon development begins, the water-holding capacity of the substrate

beneath the stand is increased, the presence of stems breaks up the force of desiccating winds, atmospheric and soil humidity are increased, the soil surface is insulated from extreme diurnal temperature fluctuations, and light filtered through the vegetative canopy is lowered in intensity and has a greater ratio of far red/red wavelengths than light incident on bare ground. In short, an entirely new habitat is created within a stand of vegetation, and it contrasts sharply to that present outside of the stand.

Clearly, the habitat in the Marshall pit is a spatial mosaic which changes over time. Some changes such as diurnal and seasonal temperature fluctuations are cyclic, but some, such as the development of closed vegetation, are directional. The variations in regeneration characteristics which were shown to exist among my 15 biennial species in the preceding section allow each of them to exploit this patchwork habitat in a different manner and, thereby, to co-exist.

The heterogeneous environment present in the Marshall pit provides many potential safe sites for seeds of all 15 species. Since a safe site, by definition, is species-specific, the occurrence of a diversity of safe sites in a habitat implies that a diversity of plant species can co-exist there. Regeneration of a given species requires that it produce viable seeds which are subsequently dispersed to safe sites. For species to co-exist, seeds of each of them must be dispersed to safe sites. A high percentage of the seeds produced by every species in my study were viable (Table 4.1). While none of these species had a dispersal vector which placed its seeds directly into safe sites, the variety of dispersal mechanisms adopted by these 15 biennial species (see 3.4 D.) did insure that the seeds of every species were

sufficiently mobile to reach safe sites within a pit where a population existed and to colonize newly created pits. Assuming that the number of potential safe sites within an area is not limiting, the abundance of a species within that area may be related to its ability to disperse its seeds to safe sites or to its production of a sufficient number of seeds to fill its potential safe sites. It has been shown that these 15 biennial species are able to disperse their seeds to available safe sites within the Marshall pit. At the time of my study every species, with the possible exception of *Arctium minus*, appeared to have ample reproductive output to fill most or all of their potential safe sites. The numbers of individuals of *Arctium minus* were apparently controlled within the study area by the actions of a seed predator which destroyed up to 75% of its annual seed production (Table 3.2).

Once a seed has been dispersed it must be able to 'detect' precisely the presence of a potential safe site. When a safe site is detected, the seed must be able to break dormancy and become stimulated to germinate. Seeds of *Arctium minus*, *Cirsium vulgare*, *Dipsacus sylvestris*, *Lactuca scariola*, *Verbascum blattaria*, and *Verbascum thapsus* are nondormant at maturity and may germinate immediately upon dispersal if they lodge in a favorable microsite. If they do not, seeds of these species rapidly become induced into secondary dormancy and become incorporated into the seed bank (see 4.4 B.). Dormant seeds of each of these species have physiological requirements for stratification which prevent their germination during winter. They also have depth-detecting mechanisms to assure that they do not germinate from too great a depth to emerge successfully and gap detecting mechanisms

to prevent their seedlings from emerging into standing vegetation where the probability of survival of the seedling will be low (see 4.4 B.). A portion of the freshly matured seeds of both *Daucus carota* and *Oenothera biennis* are capable of immediate germination, but the remainder are innately dormant. Freshly matured seeds of these species which do not lodge in a favorable microsite are induced into secondary dormancy and both these and the innately dormant seeds become incorporated into the seed bank. As with the preceding species, dormant seeds of both *Daucus carota* and *Oenothera biennis* have a requirement for stratification before they can break dormancy which prevents their germination in winter, and they also have both depth and gap detecting mechanisms which prevent their germinating from too great a depth or into standing vegetation respectively (see 4.4 B.). Virtually all seeds produced by *Alliaria petiolata*, *Echium vulgare*, *Melilotus alba*, *Melilotus officinalis*, *Onopordum acanthium*, *Tragopogon dubius*, and *Tragopogon pratensis* are innately dormant and are immediately incorporated into the seed bank. Dormant seeds of both *Tragopogon* species have a high temperature after-ripening requirement which must be satisfied before they become nondormant (see 4.4 B.). This allows seeds of these species to avoid germination during the heat of mid-summer and to exploit gaps in the vegetation created throughout the summer by drought and the activity of animals. Dormant seeds of *Alliaria petiolata*, *Echium vulgare*, and *Onopordum acanthium* have a variety of physiological dormancy mechanisms which prevent their germination in an unfavorable season. Seeds of *Melilotus* species are kept in a state of enforced dormancy by an impermeable seed coat (see 4.4 B.). They are capable of immediate germination as soon as the seed coat becomes permeable regardless of their depth of burial or the

surface conditions. The dormancy mechanism of these two species leads to high levels of pre-emergence mortality among their seeds.

These differences in germination and dormancy behavior are important ways by which plant species differentially respond to a mosaic environment and co-exist. Both Davis and Cantlon (1969) and Miles (1974) demonstrated that different plant species discriminated in their emergence not only between gap sizes but even between locations in a single gap. Gross (1985) demonstrated that while seeds of both *Verbascum thapsus* and *Oenothera biennis* responded to the intensity, duration, and quality of light, each species was very different in its manner of response. She was further able to correlate this difference with the germination behavior of these two species in the field.

Seeds of several of my biennial species (*Arctium minus*, *Daucus carota*, *Echium vulgare*, *Melilotus alba*, *Melilotus officinalis*, *Onopordum acanthium*, *Tragopogon dubius*, *Tragopogon pratensis*, *Verbascum blattaria*, and *Verbascum thapsus*) have the potential to emerge in the fall that they are are produced (Appendices I and II). Many studies have shown that seedlings which emerge in the fall incur greater mortality than those which emerge in spring, but that those which survive gain increased fecundity as a result of their head start (Ross and Harper 1972, Baskin and Baskin 1972, Arthur et al. 1973, Hawthorn and Cavers 1976, Symonides 1977, Weaver and Cavers 1979, Cook 1980, Gross 1980b, Howell 1981). This was evident in my experiments involving seedling emergence and establishment across a range of soil textures and within a range of gap sizes. In the 1:3 soil texture treatment, seedlings of *Echium vulgare* which had emerged in the fall, overgrew the

treatment the following spring (see 6.4 A.). Also in the 1:3 texture treatment many seedlings of *Lactuca scariola* which emerged in the fall became vernalized and flowered the following spring (see 6.3 E.). Seedlings of both species of *Tragopogon* which emerged in the fall in treatments throughout both experiments became vernalized and flowered the next spring (see 6.3 E.). Such pre-emption of biological space may be an important means by which some species are able to regenerate in the Marshall pit.

The 15 biennial species included in my study also differed in their ability to co-exist over time. Seeds of *Melilotus alba*, *Melilotus officinalis*, *Oenothera biennis*, *Onopordum acanthium*, *Verbascum blattaria*, and *Verbascum thapsus* are long-lived in the soil (see 4.4 D.). Once they become incorporated into a seed bank they can remain there for decades until surface conditions become favorable for breaking dormancy and subsequent emergence. Once these species have colonized an area and produced a seed crop, they will remain a part of even a closed community, at least in the seed bank, requiring only an infrequent disturbance to maintain their populations. Dormant seeds of *Alliaria petiolata*, *Arctium minus*, *Cirsium vulgare*, *Daucus carota*, *Dipsacus sylvestris*, *Echium vulgare*, and *Lactuca scariola* can remain a part of a seed bank for a few years, but unless disturbance occurs every 5 years or so, once plants of these species are excluded from the standing vegetation, they are excluded from a closed community. Seeds of *Tragopogon dubius* and *Tragopogon pratensis* are dependent on annual small-scale disturbance for their existence because their seeds remain viable in the soil for less than 1 year. If such disturbance does not occur, they are rapidly excluded from a closed community.

My investigations into the emergence and establishment of seedlings of these 15 biennial species, both in the field and under experimental conditions, revealed that they were also variable in the types of surface textures and the size of gaps in standing vegetation they could exploit. None of my species would be present in areas of the Marshall pit where gravel is as deep as 0.3m because their seedlings would fail to emerge, or if they did emerge, would fail to establish (Figure 6.8). In areas of finer to medium textured substrates, seedlings of *Arctium minus*, *Daucus carota*, *Melilotus alba*, *Oenothera biennis*, and *Verbascum thapsus* would be expected to establish in greater numbers whereas those of *Alliaria petiolata*, *Cirsium vulgare*, *Lactuca scariola*, *Onopordum acanthium*, *Tragopogon dubius*, and *Tragopogon pratensis* would be expected to establish in greater numbers in areas of medium to coarse textured substrates (Figures 6.4-6.8). Seedlings of *Dipsacus sylvestris* would be expected to establish in greater numbers in areas where there has been some rudimentary soil development, and establishment of seedlings of *Echium vulgare* should not be affected by substrate texture. Where standing vegetation is present, gaps are required for the emergence and establishment of seedlings of most of my biennial species. Seedlings of *Alliaria petiolata*, *Verbascum blattaria*, and *Verbascum thapsus* should be unable to establish in areas of closed vegetation or in small gaps, whereas those of *Arctium minus* and *Tragopogon pratensis* should be able to establish regardless of the cover. Seedlings of every other species would be expected to establish in any area in standing vegetation where gaps of at least 400cm² in area are created (Figures 6.9-6.13).

Gross and Werner (1982) and Gross (1984) reported that for 6 biennial species which occurred sequentially in time in old fields in southern Michigan, seed size was the characteristic which determined which microsites could be colonized successfully. The range of mean weights per seed present among the biennial species in my study was also related to the microsites within the Marshall pit which each species could exploit. The smallest seeded species, *Verbascum blattaria* and *Verbascum thapsus*, were excluded from coarse textured substrates because their seedlings could not emerge, and from medium and small canopy gaps because their seedlings could not compete with standing vegetation. The remaining species had large enough seeds that the seedlings they produced either had a sufficiently large root system to withstand drought (*Alliaria petiolata*, *Echium vulgare*, *Lactuca scariola*, *Melilotus alba*, *Melilotus officinalis*, *Oenothera biennis*), a sufficiently extensive shoot system to allow them to compete for resources with standing vegetation (*Cirsium vulgare*, *Dipsacus sylvestris*), or both (*Arctium minus*, *Daucus carota*, *Onopordum acanthium*, *Tragopogon dubius*, *Tragopogon pratensis*). Thus, some species were able to exploit areas within the Marshall pit which were denied to others.

Although progressive directional change in the amount of vegetative cover present within the Marshall pit could ultimately result in the exclusion of some of my biennial species from the study area, this change is slow in areas devastated by surface mining (Klemow 1982). Consequently, the 15 biennials included in my study should be able to continue to co-exist through variations in their regeneration characteristics for years to come.

7.2 Biennials in general

The first part of this discussion presented the range of variation present in life history characteristics among 15 biennial species and demonstrated how variation in these characteristics allowed their co-existence in an abandoned gravel pit. The discussion now turns to biennial species in general, focussing on the habitats in which they occur, particularly in southwestern Ontario, and concludes with a hypothesis to account for their interspecific variation in life history characteristics.

In Chapter 1 it was reported that the nature of the biennial life cycle strategy restricted the types of habitat which the species employing it can exploit. Habitats suitable for biennials cannot be completely undisturbed because these species could not regenerate beneath the closed canopy which would eventually form. Nor can these habitats be annually disturbed because such disturbance would prevent the completion of their two stage life cycle. Areas such as abandoned pits and quarries, dune systems, cedar glades, and moraines, because of their openness are suitable habitats for biennials species, but they are not optimal biennial habitats because of their relatively harsh environment and low nutrient availability. Such habitats may support a diverse biennial flora because of low levels of competition, but more produotive habitats such as grazed lands, old fields, woodland gaps and edges, chalk grasslands, and mud and shingle shores also support several biennial species. These latter habitats generally contain many more individuals of the species which are present and those individuals are more robust because of more favorable growing conditions.

The Marshall pit is not an exceptionally favorable biennial habitat, nor are gravel pits *per se* unique among habitats in southwestern Ontario in their ability to support populations of biennial plants. Prior to gravel mining however, land use throughout southwestern Ontario (agriculture and/or forests) restricted biennial species to roadsides, railroad right-of-ways, construction sites, and vacant lots, locations where they were vulnerable to weed control practices. Thus, abandoned gravel pits serve as refugia for many ruderal species, including biennials, in this area.

In all likelihood most, if not all, biennial species initially were brought into southwestern Ontario by vehicular traffic on highways, railroads, canals, and ports on Lakes Ontario, Erie, and Huron. Undoubtedly these are still major routes of dispersal for seeds of biennial species today.

Abandoned gravel pits are important refugia for biennial species in southwestern Ontario, partially because they provide an extremely heterogeneous environment which accommodates many species, and partially because they are so slow to revegetate. However, if no further mining occurs within a given pit, a dense vegetation will develop in it in time. When the foliar canopy closes, small seeded biennial species such as *Oenothera biennis*, *Verbascum blattaria*, and *Verbascum thapsus* will be excluded from the standing vegetation because the conditions necessary for breaking their seed dormancy are no longer met. Other species such as *Alliaria petiolata*, *Cirsium vulgare*, *Echium vulgare*, *Lactuca scariola*, *Melilotus alba*, *Melilotus officinalis*, and *Onopordum acanthium* will be excluded because their seedlings cannot tolerate competition from standing vegetation. A few biennial species, however, can persist in closed herbaceous vegetation for

years. *Arctium minus*, *Daucus carota*, *Tragopogon dubius*, and *Tragopogon pratensis* have seedlings that are able to tolerate competition from standing vegetation. *Dipsacus sylvestris* is able to persist under such circumstances by a combination of its dispersal and germination behavior, and the growth form of the flowering stalk. Werner (1977) showed that in old fields in southern Michigan flowering stalks of *Dipsacus sylvestris* retained a dense basal whorl of leaves. When seeds of this species were dispersed in the fall, many landed at the base of the parent and lodged beneath the basal whorl of leaves. When the flowering stalk senesced, the basal leaves left a gap in the vegetation which remained open over winter. Seedlings of *Dipsacus sylvestris* emerged into the gap created by its parent the following spring. Thus, this species created its own gaps for regeneration in standing vegetation. It can be seen then, that several biennial species will remain a part of the plant community in abandoned gravel pits for years after the herbaceous canopy has closed.

Areas such as gravel pits are among the novel habitats which were created in southwestern Ontario by European settlers. Previous to European colonization, virtually all of eastern North America was heavily forested, and open areas suitable for the growth of native ruderal species were restricted to swamps and bogs, cliffs and river bluffs, windfalls and burns, and small grassy areas such as serpentine and shale barrens, cedar glades, balds, prairie patches, and barrens of the interior lowlands (Braun 1950). The advanced cropping procedures of Indian tribes were a relatively recent phenomenon (P.B. Cavers, personal communication). When Europeans came to northeastern North America, they brought with them an assemblage of

ruderal plants which had evolved for millenia in association with the activities of man. The ancestors of the biennial species which the Europeans introduced to North America were undoubtedly plants of river banks, glacial moraines, scree slopes, and semi-arid areas (Salisbury 1961). Their life histories had predisposed them to exploit man-made disturbances such as overgrazing by domestic animals, cleared forests, the construction of roadways and towns, and mining for stone and minerals. There may in fact have been biennial species which colonized the abandoned quarries where the Egyptians cut stone for their pyramids. Old World ruderal plants, including biennial species, were pre-adapted to exploit the habitats created when European settlers cleared the forests and built their nations in North America. Few native biennial species to date have been able to colonize man-disturbed sites such as gravel pits. Of the 15 biennial species included in my study, all are introduced from the Old World except for *Oenothera biennis*. Even this species is not native to northeastern North America. It originated in Mexico (Cleland 1971) and spread across the prairies as part of a guild of fugitive species which exploited disturbances created by animals (Platt 1975). When the forests were cleared, *Oenothera biennis* was pre-adapted to migrate rapidly eastwards and exploit disturbances created by man.

Very few species are biennials. According to Hart (1977), of the 14,500 species included in the provisional checklist for Flora North America, only 1.4% were classed as biennials. One can conclude from this that the biennial strategy has seldom been selected for successfully and that biennial species have a very narrow window on the world within which they can compete against annuals and perennials. The biennial life history strategy appears

to be tightly circumscribed. Its execution inherently requires traits such as semelparity and a two stage life cycle. Yet the 15 biennial species included in my study were found to be highly variable in the characteristics which made up their regeneration niches. According to Grubb (1977), these are characteristics which should be important in determining the success of a semelparous species. One would expect close uniformity among such traits within a closely circumscribed group of species. The explanation for this variability can be found in an investigation of the results of my research. If all the life history characteristics I investigated are considered together, my three pairs of congeneric species responded similarly in each case. The remaining species however, were so variable that all attempts to group their regeneration characteristics into adaptive syndromes failed. Examination of Table 2.1 reveals that such a wide variety in life history characteristics among these biennial species is hardly unexpected. These species belong to 12 genera, which in turn are part of 8 families, which in turn represent 7 orders. Clearly, the biennial strategy has arisen independently many times in several diverse phylogenetic groups. In a large group such as the Compositae it may have arisen independently many times. There is no reason to doubt that the biennial strategy may have arisen in different groups as a common response to quite different selective forces. Since each species has a unique place of origin, ancestral habitat, and evolutionary history, as well as different genetic constraints placed upon it as a result of that unique history, it could be predicted that different species which employ the biennial life history strategy would also employ different tactics (*sensu* Harper 1977) in the execution of that strategy. Although Smith (1927) first alluded to the diverse phylogenetic origins of biennial species, only recently

have plant population ecologists begun to recognize the critical role that the evolutionary history of a species plays in the elucidation of the particular suite of life history characteristics which that species presently possesses. In her investigation of differing responses to light in the germination behavior of seeds of *Verbascum thapsus* and *Oenothera biennis*, Gross (1985) reported that these two species had very different points of origin, ancestral habitats, and evolutionary histories. She then made note that the differences in germination characteristics which she observed in these two species today could be explained by their differing evolutionary histories. Investigations into the evolutionary histories of each of the remaining 13 biennial species included in my study should prove a fruitful area from which to gain an understanding of their regeneration characteristics.

APPENDICES

Appendix I. Comparison of the mean percent (± S.D.) of seedlings present between each of 5 soil surface textures during 5 sampling periods for each of 14 biennial taxa. Values for each taxa are expressed as a percentage of the number of seeds initially sown. Entries in the same row followed by the same letter are not significantly different (P>0.05).

Alliaria petiolata

Date	100% Sand	3:1	1:1	1:3	100% Gravel
08/30/82	0a	0a	0a	0a	0a
11/10/82	0a	0a	0a	0a	0a
06/20/83	2.8 ± 2.5ab	1.5 ± 1.8ab	2.5 ± 1.6a	2.6 ± 1.8a	0b
07/25/83	1.0 ± 1.4ab	1.4 ± 2.1ab	2.5 ± 1.7a	2.4 ± 1.8a	0b
09/26/83	0.3 ± 0.3a	0.8 ± 1.2a	1.8 ± 0.9a	2.4 ± 2.4a	0a

Arctium minus

Date	100% Sand	3:1	1:1	1:3	100% Gravel
08/30/82	0a	0a	0a	0a	0a
11/10/82	3.1 ± 2.8ab	1.1 ± 1.2b	4.2 ± 4.0ab	19.6 ± 15.9a	1.5 ± 1.5b
06/20/83	6.6 ± 2.6a	10.0 ± 1.8a	8.8 ± 4.2a	2.1 ± 2.4b	0b
07/25/83	4.0 ± 2.5ab	8.2 ± 1.7a	7.4 ± 3.5a	1.2 ± 2.2bc	0c
09/26/83	2.1 ± 1.7a	1.5 ± 0.9ab	2.8 ± 1.6a	0.8 ± 1.5ab	0b

Cirsium vulgare

Date	100% Sand	3:1	1:1	1:3	100% Gravel
08/30/82	0a	0a	0a	0a	0a
11/10/82	0a	0a	0a	0a	0a
06/20/83	0.1 ± 0.2a	0.8 ± 0.9a	0.6 ± 0.8a	0.5 ± 0.4a	0a
07/25/83	0a	0.5 ± 0.4a	0.8 ± 1.0a	0.2 ± 0.5a	0a
09/26/83	0a	0a	0.6 ± 1.0a	0.2 ± 0.5a	0a

Appendix I Continued

Daucus carota

Date	100% Sand	3:1	1:1	1:3	100% Gravel
08/30/82	0a	0a	0a	0a	0a
11/10/82	12.3 ± 16.0a	6.4 ± 2.4ab	5.4 ± 1.3ab	6.0 ± 2.5ab	0.4 ± 0.4b
06/20/83	7.8 ± 3.7a	6.7 ± 1.9a	7.9 ± 2.1a	2.4 ± 1.2b	0c
07/25/83	3.6 ± 1.7a	4.6 ± 1.3a	5.9 ± 1.8a	1.2 ± 0.8b	0c
09/26/83	2.9 ± 1.5ab	2.3 ± 0.5ab	3.8 ± 0.6a	1.6 ± 0.6b	0c

Dipsacus sylvestris

Date	100% Sand	3:1	1:1	1:3	100% Gravel
08/30/82	0a	0a	0a	0a	0a
11/10/82	0a	0a	0a	0a	0a
06/20/83	2.8 ± 2.3ab	3.5 ± 1.0a	2.4 ± 1.0ab	0.8 ± 0.8bc	0c
07/25/83	2.0 ± 1.3a	2.6 ± 0.8a	2.2 ± 0.4a	0.9 ± 0.9ab	0b
09/26/83	0.9 ± 0.8a	0.6 ± 0.5a	0.4 ± 0.6a	0.6 ± 0.8a	0a

Echium vulgare

Date	100% Sand	3:1	1:1	1:3	100% Gravel
08/30/82	0a	0a	0a	0a	0a
11/10/82	4.0 ± 4.3a	3.6 ± 1.6a	5.0 ± 2.5a	8.5 ± 2.6a	3.2 ± 2.2a
06/20/83	17.1 ± 9.6a	20.1 ± 3.8a	21.4 ± 8.9a	10.5 ± 1.5a	0b
07/25/83	11.1 ± 4.3a	18.0 ± 4.5a	19.9 ± 6.5a	10.6 ± 3.8a	0b
09/26/83	8.4 ± 3.3a	10.1 ± 1.4a	11.1 ± 3.9a	8.5 ± 1.7a	0b

Appendix I Continued

Lactuca scariola

Date	100% Sand	3:1	1:1	1:3	100% Gravel
08/30/82	0a	0a	0a	0a	0a
11/10/82	0a	0a	0a	0a	0a
06/20/83	0.5 ± 1.0b	0.2 ± 0.5b	2.5 ± 1.9b	12.8 ± 8.3a	0b
07/25/83	0.5 ± 1.0b	0.8 ± 0.5b	2.8 ± 1.9ab	11.0 ± 7.1a	0b
09/26/83	0b	0.2 ± 0.5b	2.5 ± 1.7ab	6.8 ± 5.6a	0b

Melilotus spp.

Date	100% Sand	3:1	1:1	1:3	100% Gravel
08/30/82	0b	0b	0.4 ± 0.3ab	0.6 ± 0.4a	0b
11/10/82	0.2 ± 01a	0.4 ± 0.1a	0.5 ± 0.5a	0.6 ± 0.5a	0.1 ± 0.2a
06/20/83	1.8 ± 1.3a	3.1 ± 1.4a	4.3 ± 1.9a	0.2 ± 0.3b	0b
07/25/83	1.1 ± 0.7a	1.3 ± 0.5a	2.8 ± 1.5a	0.1 ± 0.1b	0b
09/26/83	0.5 ± 0.4ab	0.6 ± 0.5ab	1.1 ± 0.7a	0.1 ± 0.1bc	0c

Oenothera biennis

Date	100% sand	3:1	1:1	1:3	100% gravel
08/30/82	0a	0a	0a	0a	0a
11/10/82	0a	0a	0a	0a	0a
06/20/83	2.3 ± 1.8b	7.3 ± 1.6a	3.1 ± 1.9b	0.1 ± 0.2c	0c
07/25/83	1.6 ± 0.8b	4.7 ± 0.5a	2.3 ± 1.2b	0c	0c
09/26/83	1.2 ± 0.5a	1.2 ± 0.7a	1.4 ± 1.1a	0b	0b

Appendix I Continued

Onopordum acanthium

Date	100% sand	3:1	1:1	1:3	100% gravel
08/30/82	0a	0a	0a	0a	0a
11/10/82	0.1 ± 0.2a	0a	0a	0a	0a
06/20/83	0.4 ± 0.9a	0.6 ± 0.5a	0.7 ± 0.7a	0.8 ± 1.2a	0a
07/25/83	0b	0.3 ± 0.2ab	0.6 ± 0.6a	0.2 ± 0.0a	0b
09/26/83	0a	0a	0.1 ± 0.2a	0.1 ± 0.1a	0a

Tragopogon dubius

Date	100% sand	3:1	1:1	1:3	100% gravel
08/30/82	2.5 ± 2.5a	1.0 ± 1.2a	2.0 ± 2.8a	6.5 ± 7.9a	0a
11/10/82	1.5 ± 3.6a	3.0 ± 2.6a	2.5 ± 3.0a	7.5 ± 6.0a	0a
06/20/83	1.5 ± 3.0a	4.0 ± 3.6a	2.5 ± 1.9a	6.0 ± 4.3a	0a
07/25/83	1.5 ± 3.0a	3.0 ± 2.6a	2.0 ± 2.3a	5.5 ± 4.1a	0a
09/26/83	1.5 ± 3.0a	3.0 ± 2.6a	2.5 ± 3.0a	6.0 ± 4.3a	0a

Tragopogon pratensis

Date	100% sand	3:1	1:1	1:3	100% gravel
08/30/82	0a	0a	0a	1.0 ± 2.0a	0a
11/10/82	2.0 ± 2.3a	1.0 ± 1.2a	0a	4.0 ± 2.8a	0.5 ± 1.0a
06/20/83	1.0 ± 2.0a	1.5 ± 3.0a	0.5 ± 1.0a	2.5 ± 1.9a	0a
07/25/83	1.0 ± 2.0a	0.5 ± 1.0a	0.5 ± 1.0a	2.5 ± 1.9a	0a
09/26/83	1.5 ± 1.9a	1.5 ± 1.9a	0a	2.5 ± 1.9a	0a

Appendix I Concluded

Verbascum blattaria

Date	100% sand	3:1	1:1	1:3	100% gravel
08/30/82	0a	0a	0a	0a	0a
11/10/82	0.5 ± 1.0a	0.9 ± 0.9a	0.2 ± 0.5a	0.1 ± 0.2a	0a
06/20/83	0.1 ± 0.2a	0.2 ± 0.4a	0.1 ± 0.2a	0a	0a
07/25/83	0a	0.2 ± 0.4a	0.1 ± 0.2a	0a	0a
09/26/83	0a	0a	0a	0a	0a

Verbascum thapsus

Date	100% sand	3:1	1:1	1:3	100% gravel
08/30/82	0a	0a	0a	0a	0a
11/10/82	1.2 ± 0.7ab	2.2 ± 0.7a	0.8 ± 0.8ab	0.3 ± 0.6bc	0c
06/20/83	0b	0.2 ± 0.2a	0.2 ± 0.2a	0b	0b
07/25/83	0b	0.2 ± 0.2ab	0.4 ± 0.3a	0b	0b
09/26/83	0a	0.1 ± 0.1a	0.2 ± 0.2a	0a	0a

Appendix 11. Comparison of the mean percent (± S.D.) of seedlings of each of 14 biennial taxa which were present between each of 5 gap sizes during 5 sampling periods. Values for each taxa are expressed as a percentage of the number of seeds initially sown. Entries within a row followed by the same letter are not significantly different (P>0.05).

Alliaria petiolata

Date	40x40cm	30x30cm	20x20cm	10x10cm	No Gap
08/30/82	0a	0a	0a	0a	0a
11/10/82	0a	0a	0a	0a	0a
06/20/83	0.4 ± 0.2a	0a	0a	0.1 ± 0.2a	0.1 ± 0.2a
07/25/83	0.1 ± 0.2a	0a	0a	0.1 ± 0.2a	0a
09/26/83	0a	0a	0a	0a	0a

Arctium minus

Date	40x40cm	30x30cm	20x20cm	10x10cm	No Gap
08/30/82	0a	0a	0a	0a	0a
11/10/82	4.6 ± 5.8a	0.8 ± 0.6ab	0.2 ± 0.5ab	0b	0b
06/20/83	19.4 ± 4.2a	14.1 ± 8.6ab	9.5 ± 7.7ab	7.6 ± 4.0ab	5.1 ± 6.9b
07/25/83	20.5 ± 5.0a	18.1 ± 13.0a	11.4 ± 5.9a	18.0 ± 18.0a	14.6 ± 11.1a
09/26/83	16.0 ± 3.5a	13.0 ± 10.9a	6.6 ± 4.8a	4.6 ± 6.7a	9.6 ± 8.9a

Cirsium vulgare

Date	40x40cm	30x30cm	20x20cm	10x10cm	No Gap
08/30/82	0a	0a	0a	0a	0a
11/10/82	0a	0a	0a	0a	0a
06/20/83	8.4 ± 6.2a	6.4 ± 5.1a	5.0 ± 3.9a	2.4 ± 3.5a	0.6 ± 1.2a
07/25/83	5.6 ± 6.1a	4.2 ± 4.7a	4.4 ± 4.1a	3.1 ± 2.7a	1.1 ± 0.8a
09/26/83	3.6 ± 3.6a	3.4 ± 3.6a	2.6 ± 3.0a	0.2 ± 0.3a	0.9 ± 0.8a

Appendix II Continued

Daucus carota

Date	40x40cm	30x30cm	20x20cm	10x10cm	No Gap
08/30/82	0a	0a	0a	0a	0a
11/10/82	4.6 ± 2.5a	2.2 ± 1.4ab	2.0 ± 2.1ab	0.8 ± 0.7bc	0c
06/20/83	8.6 ± 5.4ab	11.0 ± 7.6a	8.8 ± 7.2ab	6.4 ± 4.2ab	0.4 ± 0.2b
07/25/83	6.4 ± 6.9a	5.9 ± 6.6a	6.9 ± 9.2a	2.5 ± 1.4a	0.4 ± 0.5a
09/26/83	6.6 ± 6.9a	5.1 ± 4.8a	5.8 ± 9.0a	1.7 ± 1.4a	0.4 ± 0.1a

Dipsacus sylvestris

Date	40x40cm	30x30cm	20x20cm	10x10cm	No Gap
08/30/82	0a	0a	0a	0a	0a
11/10/82	0a	0a	0a	0a	0a
06/20/83	19.2 ± 10.5a	20.0 ± 14.1ab	20.6 ± 17.3a	12.2 ± 8.7ab	0.8 ± 0.8b
07/25/83	14.2 ± 15.4a	16.2 ± 12.8a	12.5 ± 8.9a	10.6 ± 7.0a	1.4 ± 1.3a
09/26/83	9.2 ± 8.3a	5.4 ± 1.3ab	2.9 ± 2.8ab	1.0 ± 2.0b	0.6 ± 1.1b

Echium vulgare

Date	40x40cm	30x30cm	20x20cm	10x10cm	No Gap
08/30/82	0a	0a	0a	0a	0a
11/10/82	0.4 ± 0.5a	0.5 ± 0.7a	0.1 ± 0.2a	0.1 ± 0.2a	0a
06/20/83	3.2 ± 1.9a	2.1 ± 1.2ab	1.2 ± 2.2ab	0.9 ± 0.8ab	0.2 ± 0.5b
07/25/83	2.6 ± 1.6a	2.2 ± 1.2a	2.8 ± 2.0a	3.0 ± 1.9a	3.0 ± 1.6a
09/26/83	0.8 ± 0.5a	0.9 ± 1.4a	1.5 ± 2.7a	0.5 ± 0.6a	0.8 ± 0.9a

Appendix II Continued

Lactuca scariola

Date	40x40cm	30x30cm	20x20cm	10x10cm	No Gap
08/30/82	0a	0a	0a	0a	0a
11/10/82	0a	0a	0a	0a	0a
06/20/83	0.2 ± 0.5a	1.2 ± 1.3a	0.5 ± 1.0a	0a	0a
07/25/83	0.5 ± 0.6a	0.8 ± 1.0a	0.2 ± 0.5a	0a	0a
09/26/83	0a	0.2 ± 0.5a	0.2 ± 0.5a	0a	0a

Melilotus spp.

Date	40x40cm	30x30cm	20x20cm	10x10cm	No Gap
08/30/82	0.3 ± 0.2a	0.2 ± 0.2a	0.2 ± 0.2a	0.2 ± 0.1a	0.2 ± 0.2a
11/10/82	0.2 ± 0.2a	0.1 ± 0.1a	0.1 ± 0.1a	0.1 ± 0.1a	0
06/20/83	2.1 ± 1.2a	2.1 ± 1.7a	1.3 ± 1.2ab	1.2 ± 1.2ab	0.1 ± 0.2b
07/25/83	1.5 ± 1.1a	0.9 ± 0.4a	1.0 ± 1.2a	0.8 ± 0.8a	0.2 ± 0.2a
09/26/83	1.0 ± 1.0a	0.6 ± 0.4a	0.4 ± 0.8a	0.6 ± 0.8a	0.2 ± 0.1a

Oenothera biennis

Date	40x40cm	30x30cm	20x20cm	10x10cm	No Gap
08/30/82	0a	0a	0a	0a	0a
11/10/82	0a	0a	0a	0a	0a
06/20/83	1.7 ± 1.8a	1.1 ± 1.0ab	0.4 ± 0.5ab	0.2 ± 0.4ab	0b
07/25/83	0.2 ± 0.3a	0.2 ± 0.2a	0.2 ± 0.2a	1.0 ± 0.2a	0.1 ± 0.2a
09/26/83	0.4 ± 0.4a	0.1 ± 0.2a	0.6 ± 0.8a	0a	0a

Appendix II Continued

Onopordum acanthium

Date	40x40cm	30x30cm	20x20cm	10x10cm	No Gap
08/30/82	0a	0a	0a	0a	0a
11/10/82	0a	0a	0a	0a	0a
06/20/83	0.1 ± 0.1a	0a	0.1 ± 0.1a	0a	0a
07/25/83	0.1 ± 0.1a	0.1 ± 0.1a	0a	0a	0a
09/26/83	0a	0a	0.1 ± 0.1a	0a	0a

Tragopogon dubius

Date	40x40cm	30x30cm	20x20cm	10x10cm	No Gap
08/30/82	2.5 ± 2.5a	0.5 ± 1.0a	1.5 ± 1.9a	1.0 ± 2.0a	0a
11/10/82	2.0 ± 1.6a	1.0 ± 1.2a	2.0 ± 2.8a	0.5 ± 1.0a	0a
06/20/83	4.5 ± 3.4a	2.0 ± 1.6a	2.5 ± 1.0a	3.5 ± 3.0a	0.5 ± 1.0a
07/25/83	4.5 ± 1.9a	2.5 ± 1.9ab	3.5 ± 3.4ab	2.0 ± 2.3ab	0b
09/26/83	4.0 ± 1.6a	3.5 ± 2.5a	3.5 ± 3.0a	2.0 ± 2.3a	0a

Tragopogon pratensis

Date	40x40cm	30x30cm	20x20cm	10x10cm	No Gap
08/30/82	10.0 ± 11.3a	15.0 ± 10.5a	16.0 ± 1.6a	18.5 ± 10.9a	8.5 ± 6.6a
11/10/82	11.5 ± 8.1a	20.0 ± 12.5a	20.5 ± 3.4a	22.5 ± 10.6a	0.5 ± 1.0b
06/20/83	8.0 ± 7.1ab	7.5 ± 5.3ab	8.0 ± 3.6ab	10.5 ± 5.7a	1.5 ± 1.9b
07/25/83	10.0 ± 12.4a	10.0 ± 8.5a	9.0 ± 2.6a	11.0 ± 9.0a	2.5 ± 3.8a
09/26/83	11.5 ± 12.5a	14.5 ± 12.7a	14.5 ± 4.7a	12.0 ± 8.2a	7.5 ± 6.2a

Appendix II Concluded

Verbascum blattaria

Date	40x40cm	30x30cm	20x20cm	10x10cm	No Gap
08/30/82	0a	0a	0.1 ± 0.2a	0a	0a
11/10/82	0a	0a	0a	0a	0a
06/20/83	0.2 ± 0.4a	0a	0a	0a	0a
07/25/83	0a	0.1 ± 0.2a	0a	0a	0a
09/26/83	0a	0a	0a	0a	0a

Verbascum thapsus

Date	40x40cm	30x30cm	20x20cm	10x10cm	No Gap
08/30/82	0a	0a	0a	0a	0a
11/10/82	0a	0a	0.1 ± 0.1a	0a	0a
06/20/83	0a	0a	0a	0a	0a
07/25/83	0a	0.1 ± 0.1a	0a	0a	0a
09/26/83	0a	0a	0a	0a	0a

References Cited

Ackerman, E. A. 1941. The Koppen classification of climates in North America. Geogr. Rev., 31: 105-11.

Alex, J. F., and C. M. Switzer. 1976. Ontario Weeds. Ontario Agricultural College Publication 505. University of Guelph, Guelph, Ontario.

Alex, J. F., Cayouette, R., and G. A. Mulligan. 1980. Common and botanical names of weeds in Canada. Expert Committee on Weeds, Agriculture Canada, Ottawa, Ontario.

Angevine, M. W., and B. F. Chabot. 1979. Seed germination syndromes in higher plants. pp. 188-206. *In* Solbrig, O. T., Jain, S., Johnson, G. B., and P. H. Raven (eds.). Topics in Plant Population Biology. Columbia University Press, New York.

Arthur, A. G., Gale, J. S., and K. J. Lawrence. 1973. Variation in wild populations of *Papaver dubium*. VII. Germination time. Heredity, 30: 189-197.

Baker, H. G. 1974. The Evolution of weeds. Ann. Rev. Ecol. Syst., 5: 1-24.

Baker, H. G. 1972. Seed weight in relation to environmental conditions in California. Ecology, 53: 997-1010.

Baskin, J. M., and C[redacted]askin. 1981. Seasonal changes in germination responses of buried seeds of *Verbascum thapsus*, *V. blattaria* and ecological implications. Can. J. Bot., 59: 1769-1775.

Baskin, J. M., and C. C. Baskin. 1979a. Studies on the autecology and population biology of the monocarpic perennial *Grindelia lanceolata*. Am. Midl. Nat., 102: 290-299.

Baskin, J. M., and C. C. Baskin. 1979b. Studies in the autecology and population biology of the weedy monocarpic perennial, *Pastinaca sativa*. J. Ecol., 67: 601-610.

Baskin, J. M., and C. C. Baskin. 1972. Influence of germination date on survival and seed production in a natural population of *Leavenworthia stylosa*. Am. Midl. Nat., 88(2): 318-323.

Beattie, A. J., Breedlove, D. E., and P. R. Erlich. 1973. The ecology of pollinators and predators of *Frasera speciosa*. Ecology, 54: 81-91.

Beckwith, S. L. 1954. Ecological succession on abandoned farm lands and its relationship to wildlife management. Ecol. Monogr., 24: 349-376.

Bell, T. J., and J. A. Quinn. 1982. Population differences in phenology and seed germination of *Dichanthelium clandestinum* (L.) Gould (Gramineae). Bull. Ecol. Soc. Amer., 63: 130-1.

Bentley, S., Whittaker, J. B., and A. J. C. Malloch. 1980. Field experiments on the effects of grazing by a chrysomelid beetle (*Gastrophysa viridula*) on seed production and quality in *Rumex obtusifolius* and *Rumex crispus*. J. Ecol., 68: 671-74.

Black, J. N. 1958. Competition between plants of different initial seed sizes in swards of subterranean clover (*Trifolium subterraneanL.*) with

particular reference to leaf area and the light microclimate. Aust. Jour. Agric. Res., 9: 299-317.

Black, J. N. 1957. The early vegetative growth of three strains of subterranean clover (*Trifolium subterraneum L.*) in relation to size of seed. Aust. J. Agr. Res., 8: 1-14.

Black, J. N. 1956. The influence of seed size and depth of sowing on preemergence and early vegetative growth of subterrean clover (*Trifolium subterraneum* L.). Aust. J. Agric. Res., 7: 98-109.

Bramble, W. C., and R. H. Ashley. 1955. Natural revegetation of spoil banks in central Pennsylvania. Ecology, 36: 417-23.

Braun, E. L. 1950. Deciduous Forests of Eastern North America. (Reprinted by Hafner, New York, 1967.)

Breeman, A. M. M. van. 1984. Comparative germination ecology of three short-lived monocarpic Boraginaceae. Acta Bot. Neerl., 33(3): 283-305.

Breeman, A. M. M. van, and B. H. van Leeuwen. 1983. The seed bank of three short-lived monocarpic species, *Cirsium vulgare* (Compositae), *Echium vulgare* and *Cynoglossum officinale* (Boraginaceae). Acta Bot. Neerl., 32: 245-246.

Brown, J. H., Reichman, O. J., and D. W. Davidson. 1979. Granivory in desert ecosystems. Ann. Rev. Ecol. Syst., 10: 201-227.

Bullock, S. H., and R. B. Primack. 1977. Comparative experimental study of seed dispersal on animals. Ecology, 58: 681-86.

Byrnes, W. R., and J. H. Miller. 1973. Natural revegetation and cast overburden properties of surface-mined coal lands in southern Indiana, pp. 285-305. *In* Ecology and Reclamation of Devastated Land, Vol. 1. R. J. Hutnik and G. Davis (eds.). Gordon and Breach, New York.

Campbell, M. H., and F. G. Swain. 1973. Effect of strength, tilth, and heterogeneity of the soil surface on radicle-entry of surface-sown seeds. J. Br. Grassld. Soc., 28: 41-50.

Caruso, J. L. 1970. Early seedling survival of *Melilotus* in bluegrass sod. Ecology, 51(3): 553-554.

Caswell, H. 1982. Life history theory and the equilibrium status of populations. Am. Nat., 120: 317-39.

Caswell, H., and P. A. Werner. 1978. Transient behavior and life history analysis of teasel (*Dipsacus sylvestris* Huds.). Ecology, 59: 53-66.

Cavers, P. B. 1983. Seed demography. Can. J. Bot., 61: 3578-3590.

Cavers, P. B., and M. G. Steel. 1984. Patterns of change in seed weight over time on individual plants. Am. Nat., 124: 324-35.

Cavers, P. B., and J. L. Harper. 1967a. Studies in the dynamics of plant populations. I. The fate of seed and transplants introduced into various habitats. J. Ecol., 55: 59-71.

Cavers, P. B., and J. L. Harper. 1967b. The comparative biology of closely related species living in the same area. IX. *Rumex*: the nature of adaptation to sea-shore habitat. J. Ecol., 55: 73-81.

Cavers, P. B., and J. L. Harper. 1966. Germination polymorphism in *Rumex crispus* and *Rumex obtusifolius*. J. Ecol., 54: 367-82.

Cavers, P. B., Heagy, M. I., and R. F. Kokron. 1979. The biology of Canadian weeds 35. *Alliaria petiolata* (M.Bieb) Cavara and Grande. Can. J. Plant Soc., 59: 217-229.

Champness, S. S., and K. Morris. 1948. The population of buried viable seeds in relation to contrasting pasture and soil types. J. Ecol., 36: 149-173.

Chapman, L. J., and D. F. Putnam. 1966. The physiography of southern Ontario. Second edition. University of Toronto Press, Toronto.

Charnov, E. L., and W. M. Schaffer. 1973. Life history consequences of natural selection: Cole's result revisited. Am. Nat., 107: 791-92.

Chepil, W. S. 1946. Germination of weed seeds. I. Longevity, periodicity of germination, and vitality of seeds in cultivated soil. Sci. Agric., 26: 307-346.

Cideciyan, M. A., and A. J. C. Malloch. 1982. Effects of seed size on the germination, growth, and competitive ability of *Rumex crispus* and *Rumex obtusifolius*. J. Ecol., 70: 227-32.

Cleland, R. E. 1972. *Oenothera* cytogenetics and evolution. Academic Press, New York. 370 pp.

Cook, R. E. 1980. Germination and size-dependent mortality in *Viola blanda*. Oecologia (Berl.), 47: 115-117.

Cook, R. E. 1979. Patterns of juvenile mortality and recruitment in plants. *In* Topics in Plant Population Biology, O. T. Solbrig, S. Jain, G. B. Johnson, and P. H. Raven. (eds.). pp. 207-231. Columbia University Press, New York.

Cook, R. E. 1975. The photoinductive control of seed weight in *Chenopodium rubrum* L. Am. J. Bot., 62: 427-31.

Crocker, W. 1938. Life-span of seeds. Bot. Rev., 4: 235-274.

Croxton, W. C. 1928. Revegetation of Illinois coal-stripped land. Ecology, 9: 155-75.

Dale, H. M. 1974. The biology of Canadian weeds 5. *Daucus carota*. Can. J. Plant Sci., 54: 673-685.

Dale, H. M., and P. J. Harrison. 1966. Wild carrot seeds: germination and dormancy. Weeds, 14: 201-204.

Darlington, H. T., and G. P. Steinbauer. 1961. The eighty year period for Dr. Beal's seed viability experiment. Am. J. Bot., 48: 321-325.

Darwin, C. 1860. On the Origin of Species by Means of Natural Selection, or The Preservation of Favoured races in the Struggle for Life. American edition. D. Appleton and Company, New York.

Davis, R. M., and J. E. Cantlon. 1969. Effect of size area open to colonization on species composition in early old field succession. Bull. Torrey Bot. Cl., 96: 660-673.

Dore, W. G., and L. C. Raymond. 1942. Pasture studies. XXIV. Viable seeds in pasture soil and manure. Sci. Agric., 23: 69-79.

Dorph-Peterson, K. 1925. Examinations of the occurrence and vitality of various weed seed species under different conditions, made at the Danish State Seed Testing Station during the years 1896-1923. Reports at the Fourth International Seed Testing Congress. Cambridge: Published by His Majesty's Stationary Office.

Dowling, P. M., Clements, R. J., and J. R. McWilliam. 1971. Establishment and survival of pasture species from seed sown on the soil surface. Australian Research, 22: 61-74.

Environment Canada. 1983. Annual meteorological summary. Atmospheric Environment Service, Ottawa, Ontario.

Environment Canada. 1982. Annual meteorological summary. Atmospheric Environment Service, Ottawa, Ontario.

Environment Canada. 1981a. Canadian climate normals, temperature and precipitation, Ontario, 1951-1980. Atmospheric Environment Service, Ottawa, Ontario.

Environment Canada. 1981b. Annual meteorological summary. Atmospheric Environment Service, Ottawa, Ontario.

Evans, R. A., and J. A. Young. 1972. Microsite requirements for establishment of annual rangeland weeds. Weed Sci., 20: 350-356.

Evenari, M., Koller, D., and Y. Gutterman. 1966. Effects of the environment of the mother plant on germination by control of seed-coat permeability to water in *Ononis sicula* Guss. Aust. J. Biol. Sci., 19: 1007-16.

Everson, L. 1949. Preliminary studies to establish laboratory methods for the germination of weed seed. Proceedings of the Association of Official Seed Analysts. Thirty-ninth meeting. Published by the Association.

Fenner, M. 1985. Seed Ecology. Chapman and Hall, London.

Fenner, M. 1983. Relationships between seed weight, ash content, and seedling growth in twenty-four species of Compositae. New Phytol., 95: 697-706.

Fenner, M. 1978. A comparison of the abilities of colonizers and closed-turf species to establish from seed in artificial swards. J. Ecol., 66: 953-963.

Fuller, W., Hance, C. E., and M. J. Hutchings. 1983. Within-season fluctuations in mean fruit weight in *Leontodon hispidus* L. Ann. Bot., 51: 545-49.

Gadgil, M. 1970. Dispersal: population consequences and evolution. Ecology, 52: 253-61.

Gadgil, M. D., and W. H. Bossert. 1970. Life history consequences of natural selection. Am. Nat., 104: 1-24.

Gardner, W. A. 1921. Effect of light on germination of light-sensitive seeds. Bot. Gaz., 71: 249-288.

Gleason, H. A., and A. Cronquist. 1963. Manual of vascular plants of northeastern United States and adjacent Canada. D. van Nostrand Co., New York.

Goldberg, D. E., and P. A. Werner. 1983. The effects of size of opening in vegetation and litter cover on seedling establishment of goldenrods (*Solidago* spp.). Oecologia (Berl.), 60: 149-155.

Gorski, T., Gorska, K. and J. Nowicki. 1977. Germination of seeds of various herbaceous species under leaf canopy. Flora, 166: 249-259.

Gorski, T., Gorska, K., and J. Rybicki. 1978. Studies on the germination of seeds under leaf canopy. Flora, 167: 289-299.

Grant-Lipp, A. E., and L. A. T. Ballard. 1963. Germination patterns shown by the light-sensitive seed of *Anagallis arvensis*. Aust. J. Biol. Sci., 16: 572-84.

Gray, D. 1979. The germination response to temperature of carrot seeds from different umbels and times of harvest of the seed crop. Seed Sci. Technol., 7: 169-78.

Grime, J. R. 1979. Plant strategies and vegetation processes. John Wiley and Sons, New York.

Grime, J. R., Mason, G., Curtis, A. V., Rodman, J., Band, S. R., Mowforth, M. A. G., Neal, A. M., and S. Shaw. 1981. A comparative study of germination characteristics in a local flora. J. Ecol., 69: 1017-1059.

Groh, H. 1930. Concerning the burdock seed gelechid. Can. Field Nat., 44: 21.

Gross, K. L. 1985. Effects of irradiance and spectral quality on the germination of *Verbascum thapsus* L. and *Oenothera biennis* L. seeds. New Phytol., 101: 531-541.

Gross, K. L. 1984. Effects of seed size and growth form on seedling establishment of six monocarpic plants. J. Ecol., 72: 369-387.

Gross, K. L. 1981. Predictions of fate from rosette size in four "biennial" plant species: *Verbascum thapsus*, *Oenothera biennis*, *Daucus carota*, and *Tragopogon dubius*. Oecologia (Berl.), 48: 209-213.

Gross, K. L. 1980a. Ecological consequences of differences in life history characteristics among four "biennial" plant species. Ph.D. thesis. Michigan State University, East Lansing, Michigan.

Gross, K. L. 1980b. Colonization by *Verbascum thapsus* (Mullein) of an old-field in Michigan: experiments on the effects of vegetation. J. Ecol., 68: 919-927.

Gross, K. L., and P. A. Werner. 1982. Colonizing abilities of "biennial" plant species in relation to ground cover: implications for their distributions in a successional sere. Ecology, 63(4): 921-931.

Gross, K. L., and P. A. Werner. 1978. The biology of Canadian weeds 28: *Verbascum thapsus* L. and *Verbascum blattaria* L.. Can. J. Plant Sci., 58: 401-413.

Gross, R. S., and P. A. Werner. 1983. Probabilities of survival and reproduction relative to rosette size in common burdock (*Arctium minus*: Compositae). Am. Midl. Nat., 109(1): 184-193.

Gross, R. S., Werner, P. A., and W. R. Hawthorn. 1980. The biology of Canadian weeds 38. *Arctium minus* (Hill) Bernh. and *A. lappa* L. Can. J. Plant Sci., 60: 621-634.

Grubb, P. J. 1977. The maintenance of species-richness in plant communities: the importance of regeneration niche. Biol. Rev., 52: 107-145.

Grubb, P. J. 1976. A theoretical background to the conservation of ecologically distinct groups of annuals and biennials in the chalk grassland ecosystem. Biol. Conservation, 10: 53-76.

Gutterman, Y. 1980/81. Influences on seed germinability: phenotypic maternal effects during seed maturation. Israel J. Bot., 29: 105-17.

Hamly, D. H. 1932. Softening of seeds of *Melilotus alba*. Bot. Gaz., xciii: 345-74.

Harper, J. L. 1977. Population Biology of Plants. New York: Academic Press. pp. 842.

Harper, J. L. 1967. A Darwinian approach to plant ecology. J. Ecol., 55: 242-70.

Harper, J. L., and J. White. 1974. The demography of plants. Ann. Rev. Ecol. Syst., 5: 419-463.

Harper, J. L., and J. N. Clatworthy. 1963. The comparative biology of closely related species. VI. Analysis of the growth of *Trifolium repens* and

T. fragiferum in pure and mixed populations. J. Exp. Bot., 14: 172-90.

Harper, J. L., and A. P. Chancellor. 1959. The comparative biology of closely related species living in the same area. IV. *Rumex*: interference between individuals in populations of one and two species. J. Ecol., 47: 679-695.

Harper, J. L., Lovell, P. H., and K. G. Moore. 1970. The sizes and shapes of seeds. Ann. Rev. Ecol. Syst., 1: 327-356.

Harper, J. L., Williams, J. T., and G. R. Sagar. 1965. The behaviour of seeds in soil. I. The heterogeneity of soil surfaces and its role in determining the establishment of plants from seed. J. Ecol., 53: 273-286.

Hart, R. 1977. Why are biennials so few? Am. Nat., 111: 792-99.

Hartgerink, A. P., and F. A. Bazzaz. 1984. Seedling-scale environmental heterogeneity influences individual fitness and population structure. Ecology, 65: 198-206.

Hastings, A., and H. Caswell. 1979. Role of environmental variability in the evolution of life history strategies. Proc. Natl. Acad. Sci., 76: 4700-03.

Hawthorn, W. R. 1973. Population dynamics of two weedy perennials, *Plantago major* L. and *P. rugelii* Decne. Ph.D. thesis, University of Western Ontario, London.

Hawthorn, W. R., and P. D. Hayne. 1978. Seed production and predispersal seed predation in the biennial composite species *Arctium minus* (Hill) Bernh. and *Arctium lappa* L. Oecologia (Berl.), 34: 283-295.

Hawthorn, W. R., and P. B. Cavers. 1976. Population dynamics of the perennial herbs *Plantago major* L. and *P. rugelii* Decne. J. Ecol., 64: 511-527.

Heagy, M. I. 1981. Natural vegetation of gravel pit slopes, London, Ontario. M.Sc. thesis. University of Western Ontario.

Hendrix, S. D. 1979. Compensatory reproduction in a biennial herb following insect defoliation. Oecologia (Berl.), 42: 107-118.

Hewitt, D. F., and W. R. Cowan. 1969. Sand and gravel in southern Ontario, 1967-68. Ontario Department of Mines, IMR 29. Toronto.

Hickman, J. C. 1979. The basic biology of plant numbers. *In* Topics in plant population biology. Edited by O. T. Solbrig, S. Jain, G. B. Johnson, and P. H. Raven. Columbia University Press, New York. pp. 232-263.

Hirose, T. 1983. A graphical analysis of life history evolution in biennial plants. Bot. Mag. (Tokyo), 96: 37-47.

Holt, B. R. 1972. Effect of arrival time on recruitment, mortality, and reproduction in successional plant populations. Ecology, 53(4): 668-673.

Howe, H. F., and J. Smallwood. 1982. Ecology of seed dispersal. Ann. Rev. Ecol. Syst., 13: 201-28.

Howell, N. 1981. The effect of seed size and relative emergence time on fitness in a natural population on *Impatiens capensis* Meerb. (Balsaminaceae). Am. Midl. Nat., 105: 312-320.

Inouye, D. W., and O. R. Taylor. 1980. Variation in generation time in *Frasera speciosa* (Gentianaceae), a long-lived perennial monocarp. Oecologia (Berl.), 47: 171-74.

Isikawa, S. 1954. Light sensitivity against germination. I. photoperiodism of seeds. Bot. Mag. (Tokyo), 67: 51-56.

Janzen, D. H. 1984. Dispersal of small seeds by big herbivores: foliage is the fruit. Am. Nat., 123: 338-353.

Janzen, D. H. 1976. Why bamboos wait so long to flower. Ann. Rev. Ecol. Syst., 7: 347-91.

Janzen, D. H. 1971. Seed predation by animals. Ann. Rev. Ecol. Syst., 2: 465-492.

Jong, T. J. de, and P. G. L. Klinkhammer. 1986. Population ecology of the biennials *Cirsium vulgare* and *Cynoglossum officinale*: an experimental and theoretical approach. Ph.D. thesis, Rijksuniversiteit Leiden, the Netherlands.

Kawano, S., and Y. Nagai. 1975. The productive and reproductive biology of flowering plants. I. Life history strategies of three *Allium* species in Japan. Bot. Mag. (Tokyo), 88: 281-318.

Kelly, D. 1985a. On strict and facultative biennials. Oecologia (Berl.), 67: 292-94.

Kelly, D. 1985b. Why are biennials so maligned? Am. Nat., 125: 473-79.

King, T. J. 1977a. The plant ecology of ant-hills in calcareous grasslands. I. Patterns of species in relation to ant-hills in southern England. J. Ecol., 65: 235-256.

King, T. J. 1977b. The plant ecology of ant-hills in calcareous grasslands. III. Factors affecting population sizes of selected species. J. Ecol., 65: 279-318.

King, T. J. 1975. Inhibition of seed germination under leaf canopies in *Arenaria serpyllifolia*, *Veronica arvensis*, and *Cerastium holosteoides*. New Phytol., 75: 87-90.

Kivilaan, A. 1975. Skotodormancy in *Verbascum blattaria* seed. Flora, 164: 1-5.

Kivilaan, A., and R. S. Bandurski. 1981. The one hundred year period for Dr. Beal's seed viability experiment. Am. J. Bot., 68: 1290-1292.

Kjaer, A. 1948. Germination of buried and dry stored seeds. II. 1934-1944. Proceedings of the International Seed Testing Association, 14: 19-26.

Klemow, K. M. 1982. Demography and seed biology of monocarpic herbs colonizing an abandoned limestone quarry. Ph.D. thesis. State University of New York College of Environmental Science and Forestry, Syracruse, New York.

Klemow, K. M., and D. J. Raynal. 1985. Demography of two facultative biennial plant species in an unproductive habitat. J. Ecol., 73: 147-167.

Klemow, K. M., and D. J. Raynal. 1981. Population ecology of *Melilotus alba* in a limestone quarry. J. Ecol., 69: 33-44.

Klinkhammer, P. G. L., and T. J. de Jong. 1983. Is it profitable for biennials to live longer than two years? Ecological Modelling, 20: 223-32.

Koller, D. and N. Roth. 1964. Studies on the ecological and physiological significance of amphicarpy in *Gymnarrhena micrantha* (Compositae). Am. J. Bot., 51: 26-35.

Lacey, E. P. 1982. Timing of seed dispersal in *Daucus carota*. Oikos, 39: 83-91.

Lacey, E. P. 1981. Seed dispersal in wild carrot (*Daucus carota*). Mich. Bot., 20: 15-20.

Lacey, E. P., and R. Pace. 1983. Effect of parental flowering and dispersal times on offspring fate in *Daucus carota* (Apiaceae). Oecologia (Berl.), 60: 274-278.

Lacey, E. P., Real, L., Antonovics, J., and D. G. Heckel. 1983. Variance models in the study of life histories. Am. Nat., 122: 114-31.

Leeuwen, B. H. van. 1981. Influence of micro-organisms on the germination of the monocarpic *Cirsium vulgare* in relation to disturbance. Oecologia (Berl.), 48: 112-115.

Leeuwen, B. H. van, and A. M. M. van Breemen. 1980. Similarities and differences in some biennials. Acta Bot. Neerl., 29: 209-210.

Levin, D. A., and H. W. Kerster. 1974. Gene flow in seed plants. Evol. Biol., 7: 139-220.

Louvett-Doust, J. 1980. A comparative study of life history and resource allocation in selected Umbellifereae. Biol. J. Linn. Soc., 13: 139-54.

Machlis, L., and J. G. Torrey. 1956. Plants in action. A laboratory manual of plant physiology. W. H. Freeman and Co., Inc., San Francisco.

Mack, R. N. 1976. Survivorship of *Cerastium atrovirens* at Aberffraw, Anglesey. J. Ecol., 64: 309-12.

Maguire, J. D., and A. Overland. 1959. Laboratory germination of seeds of weedy and native plants. Washington Agric. Exp. St. Station Circular 349. 15 pp.

Malone, C. R. 1967. A rapid method for enumeration of viable seeds in soil. Weeds, 15: 381-382.

Marks, M. K., and S. D. Prince. 1982. Seed physiology and seasonal emergence of wild lettuce *Lactuca scariola*. Oikos, 38: 242-249.

Marks, M. K., and S. Prince. 1981. Influence of germination date on survival and fecundity in wild lettuce *Lactuca scariola*. Oikos, 36: 326-330.

Martin, J. N. 1943. Germination studies of the seeds of some common weeds. Iowa Acad. Sci. Proc., 50: 221-228.

Maun, M. A., and P. B. Cavers. 1971. Seed production and dormancy in *Rumex crispus*. I. The effects of removal of cauline leaves at anthesis. Can.

J. Bot., 49: 1123-30.

McKay, S. M., and P. M. Catling. 1979. Trees, shrubs, and flowers to know in Ontario. J. M. Dent and sons (Canada) ltd., Oshawa, Ontario.

McWilliams, E. L., Landers, R. Q., and J. P. Mahlstede. 1968. Variation in seed weight and germination in populations of *Amaranthus retroflexus* L. Ecology, 49: 290-96.

Meijden, E. van der, and R. E. van der Waals-Kooi. 1979. The population ecology of *Senecio jacobea* in a sand dune system. I. Reproductive strategy and the biennial habit. J. Ecol., 67: 131-153.

Miles, J. 1974. Effects of experimental interference with stand structure on establishment of seedlings in *Callunetum*. J. Ecol. 62: 675-685.

Milton, W. E. J. 1943. The buried viable-seed content of a Midland calcareous clay soil. Empire J. Exp. Agric., 11: 155-167.

Mittelbach, G. G., and K. L. Gross. 1984. Experimental studies of seed predation in old fields. Oecologia (Berl.), 65: 7-13.

Naylor, R. E. L. 1972. Aspects of the population dynamics of the weed *Alopecurus myosuroides* Huds. in winter cereal crops. Jour. App. Ecol., 9: 127-139.

Oomes, M. J. M., and W. T. Elberse. 1976. Germination of six grassland herbs in microsites with different water contents. J. Ecol., 64: 745-755.

Oosting, H. J., and M. E. Humphreys. 1940. Buried viable seeds in a successional series of old field and forest soils. Bull. Torrey Bot. Cl., 67: 253-273.

Pareja, M. R., and D. W. Staniforth. 1985. Seed-soil microsite characteristics in relation to weed seed germination. Weed Sci., 33: 190-195.

Pijl, L. van der. 1982. Principles of Dispersal in Higher Plants. Third Edition. Springer-Verlag, Berlin.

Pitelka, L. F., Thayer, M. E., and S. B. Hansen. 1983. Variation in achene weight in *Aster acuminatus*. Can. J. Bot., 61: 1415-20.

Platt, W. J. 1975. The colonization and formation of equilibrium plant species associations on badger disturbances in a tall-grass prairie. Ecol. Monogr., 45: 285-305.

Platt, W. J., and I. M. Weiss. 1977. Resource partitioning and competition within a guild of fugitive prairie species. Am. Nat., 111: 479-513.

Poole, A. L., and D. Cairns. 1940. Botanical aspects of ragwort (*Senecio jacobaea* L.) control. Bull. N. Z. Dept. Sci. Industr. Res., 82: 1-66.

Popay, A. I., and E. H. Roberts. 1970. Factors involved in the dormancy and germination of *Capsella bursa-pastoris* (L.) Medik, and *Senecio vulgaris* L. J. Ecol., 58: 103-22.

Primack, R. B., and J. Antonovics. 1981. Experimental ecological genetics in *Plantago*. V. Components of seed yield in the ribwort plantain *Plantago lanceolata* L. Evolution, 35: 1069-79.

Prince, S. D., and M. K. Marks. 1982. Induction of flowering in wild lettuce (*Lactuca scariola L.*). III. Vernalization-devernalization cycle in buried seeds. New Phytol., 91: 661-668.

Prince, S. D., Marks, M. K., and R. N. Carter. 1978. Induction of flowering in wild lettuce (*Lactuca scariola* L.). New Phytol., 81: 265-277.

Rabinowitz, D. 1981. Buried viable seeds in a North American tall-grass prairie: The resemblance of their abundance and composition to dispersing seeds. Oikos, 36: 191-195.

Rabinowitz, D., and J. K. Rapp. 1980. Seed rain in a North American tall grass prairie. J. Appl. Ecol., 17: 793-802.

Radvanyi, A. 1974. Survey and control of small mammal populations on two hardwood plantations in southern Ontario. For. Chron., 50: 1-5.

Reed, F. C., and S. N. Stephenson. 1973. Factors affecting seed number and size in burdock, *Arctium minus* Schk. Mich. Acad., 5: 449-55.

Reed F. C., and S. N. Stephenson. 1972. The effects of simulated herbivory on *Ambrosia artemisiifolia* L. and *Arctium minus* Schk. Mich. Acad., 4: 359-64.

Regehr, D. L., and F. A. Bazzaz. 1979. On the population dynamics of *Erigeron canadensis*, a successional winter annual. J. Ecol., 64: 745-55.

Reinartz, J. A. 1984a. Life history variation of common mullein (*Verbascum thapsus*). I. Latitudinal differences in population dynamics and timing of reproduction. J. Ecol., 72: 897-912.

Reinartz, J. A. 1984b. Life history variation of common mullein (*Verbascum thapsus*). III. Differences among sequential cohorts. J. Ecol., 72: 927-936.

Ridley, H. N. 1930. The Dispersal of Plants Throughout the World. Reeve, Ashford.

Roberts, H. A. 1981. Seed banks in soils. Adv. Appl. Biol., 6: 1-55.

Roberts, H. A., and J. E. Neilson. 1981. Seed survival and periodicity of seedling emergence in twelve weedy species of the Compositae. Ann. Appl. Biol., 97: 325-334.

Roberts, H. A., and R. J. Chancellor. 1979. Periodicity of seedling emergence and achene survival in some species of *Carduus*, *Cirsium*, and *Onopordum*. J. Appl. Ecol., 16: 641-647.

Roberts, H. A., and M. E. Ricketts. 1979. Quantitative relationships between weed flora after cultivation and the seed population in the soil. Weed Res., 19: 269-275.

Roberts, H. A., and P. M. Feast. 1973. Emergence and longevity of seeds of annual weeds in cultivated and undisturbed soil. J. Appl. Ecol., 10: 133-143.

Roberts, H. A., and P. A. Dawkins. 1967. Effect of cultivation on the numbers of viable weed seeds in soil. Weed Res., 7: 290-301.

Ross, M. A., and J. L. Harper. 1972. Occupation of biological space during seedling establishment. J. Ecol., 60: 77-88.

Rowe, J. S. 1972. Forest Regions of Canada. Canadian Forestry Service Publication 1300. Department of the Environment, Ottawa, Ontario.

Ryvarden, L. 1971. Studies in seed dispersal. I. Trapping of diaspores in the alpine zone at Finse, Norway. Norwegian J. Bot., 18: 215-226.

Sagar, G. R., and A. M. Mortimer. 1976. An approach to the study of the population dynamics of plants with special reference to weeds. Appl. Biol., 1: 1-47.

Salisbury, E. J. 1961. Weeds and aliens. London, Collins St. James Place. 384 pp.

Salisbury, E. J. 1942. The reproductive capacity of plants. London: Bell.

Sarukhan, J. 1974. Studies on plant demography: *Ranunculus repens* L., *R. bulbosus* L., and *R. acris* L. II. Reproductive strategies and seed population dynamics. J. Ecol., 62: 151-177.

Sarukhan, J., and J. L. Harper. 1973. Studies on plant demography: *Ranunculus repens* L., *R. bulbosus* L., and *R. acris* L. I. Population flux and survivorship. J. Ecol., 61: 675-716.

SAS Institute Inc. 1982. SAS USER's Guide: Statistics, 1982 ed. Cary, N.C.: SAS Institute Inc. 584 pp.

Schaal, B. A. 1980. Reproductive capacity and seed size in *Lupinus texensis*. Am. J. Bot., 67: 703-09.

Schaffer, W. M., and M. D. Gadgil. 1975. Selection for optimal life histories in plants. pp. 142-57. *In*: Cody, M. L., and J. M. Diamond (eds.). Ecology and Evolution of Communities. Belknap Press, Cambridge, Mass.

Schimpf, D. J. 1977. Seed weight of *Amaranthus retroflexus* in relation to moisture and length of growing season. Ecology, 58: 450-53.

Schramm, J. R. 1966. Plant colonization studies on black wastes from anthracite mining in Pennsylvania. Trans. Amer. Phil. Soc., 56: 1-194.

Scifres, C. J., and M. K. McCarty. 1969. Some factors affecting germination and seedling growth of Scotch thistles. Res. Bull. Nebraska Agric. Exp. St. 228.

Semenza, R. J., Young, J. A., and R. A. Evans. 1978. Influence of light and temperature on the germination and seedbed ecology of common mullein (*Verbascum thapsus*). Weed Sci., 26: 577-581.

Sharitz, R. R., and J. F. McCormick. 1973. Population dynamics of two competing annual plant species. Ecology, 54: 723-40.

Sheldon, J. C. 1974. The behaviour of seeds in soil. III. The influence of seed morphology and behaviour of seedling on the establishment of plants from surface-lying seeds. J. Ecol., 62: 47-66.

Sheldon, J. C., and F. M. Burrows. 1973. The dispersal effectiveness of the achene pappus units of selected Compositae in steady winds with convection. New Phytol., 72: 665-75.

Silvertown, J. W. 1984a. Death of the elusive biennial. Nature, 310: 271.

Silvertown, J. W. 1984b. Phenotypic variety in seed germination behavior: the ontogeny and evolution of somatic polymorphism in seeds. Am. Nat., 124: 1-16.

Silvertown, J. W. 1983. Why are biennials sometimes not so few? Am. Nat., 121: 448-53.

Silvertown, J. W. 1982. Introduction to plant population ecology. New York: Longman. 209 pp.

Silvertown, J. W. 1981. Micro-spatial heterogeneity and seedling demography in species-rich grassland. New Phytol., 88: 117-128.

Silvertown, J. W. 1980. Leaf-canopy-induced seed dormancy in a grassland flora. New Phytol., 85: 109-118.

Silvertown, J. W., and J. B. Dickie. 1981. Seedling survivorship in natural populations of nine perennial chalk grassland plants. New Phytol., 88: 555-558.

Smith, H. B. 1927. Annual versus biennial growth habit and its inheritance in *Melilotus alba*. Am. J. Bot., 14: [illegible].

Sokal, R. R., and F. J. Rohlf. 1981. Biometry Second Edition. New York: W. H. Freeman and Company. 859 pp.

Stanton, M. L. 1985. Seed size and emergence time within a stand of wild radish (*Raphanus raphanistrum* L.): the establishment of a fitne[illegible]

hierarchy. Oecologia (Berl.), 67: 524-31.

Stanton, M. L. 1984. Seed variation in wild radish: effect of seed size on components of seedling and adult fitness. Ecology, 65: 1105-12.

Stebbins, G. L. 1971. Adaptive radiation of reproductive characteristics in angiosperms. II. Seeds and seedlings. Ann. Rev. Ecol. Syst., 2: 237-60.

Steinbauer, G. P., and B. Grigsby. 1957. Interaction of temperature, light and moistening agent in the germination of weed seeds. Weeds, 5: 175-183.

Steiner, E. 1968. Dormant seed environment in relation to natural selection in *Oenothera*. Bull. Torr. Bot. Cl., 95: 140-155.

Stergios, B. G. 1976. Achene production, dispersal, seed germination and seedling establishment of *Hieracium aurantiacum* in an abandoned field community. Can. J. Bot. 54: 1189-97.

Stevens, O. A. 1957. Weights of seeds and numbers per plant. Weeds, 5: 46-55.

Stevens, O. A. 1932. The number and weight of seeds produced by weeds. Am. J. Bot., 19: 784-794.

Symonides, E. 1977. Mortality of seedlings in natural psammophyte populations. Ekol. Pol., 25(4): 635-651.

Thompson, K. 1984. Why biennials are not as few as they ought to be. Am. Nat., 123: 854-61.

Thompson, K., and J. P. Grime. 1983. A comparative study of germination responses to diurnally fluctuating temperatures. J. Appl. Ecol., 20: 141-156.

Thompson, K., and J. P. Grime. 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. J. Ecol., 67: 893-921.

Thompson, P. A. 1981. Variation in seed size within populations of *Silene dioica* (L.) Clariv. in relation to habit. Ann. Bot., 47: 623-34.

Threadgill, P. F., Baskin, J. M., and C. C. Baskin. 1981. The ecological life cycle of *Frasera caroliniensis*, a long-lived monocarpic perennial. Am. Midl. Nat., 105: 277-89.

Toole, E. H., and E. Brown. 1946. Final results of the Duvel buried seed experiment. J. Agric. Res., 72: 201-210.

Toole, E. H., Toole, V. K., Hendricks, S. B., and H. A. Borthwick. 1957. Effect of temperature on the germination of light sensitive seeds. Proceedings of the International Seed Testing Association, 22: 196-204.

Turkington, R. A., Cavers, P. B., and E. Rempel. 1978. The biology of Canadian weeds 29. *Melilotus alba* Desr. and *M. officinalis* (L.) Lam. Can. J. Plant Sci., 58: 523-537.

Turner, R. M., Alcorn, S. M., Olin, G., and J. A. Booth. 1966. The influence of shade, soil and water on saguaro seedling establishment. Bot. Gaz., 127: 95-102.

Venable, D. L., and D. A. Levin. 1985. Ecology of achene dimorphism in *Heterotheca latifolia*. I. Achene structure, germination, and dispersal. J. Ecol., 73: 133-45.

Verkaar, H. J., and A. J. Schenkeveld. 1984a. On the ecology of short-lived forbs in chalk grasslands: life history characteristics. New Phytol., 98: 659-72.

Verkaar, H. J., and A. J. Schenkeveld. 1984b. On the ecology of short-lived forbs in chalk grasslands: semelparity and seed output of some species in relation to various levels of nutrient supply. New Phytol., 98: 673-82.

Viereck, L. A. 1966. Plant succession and soil development on gravel outwash of the Muldrow Glacier, Alaska. Ecol. Monogr., 36: 181-99.

Waller, D. M. 1982. Factors influencing seed weight in *Impatiens capensis* (Balsaminaceae). Am. J. Bot., 69: 1470-75.

Watkinson, A. R. 1978. The demography of a sand dune annual: *Vulpia fasciculata*. II. The dynamics of seed populations. J. Ecol., 66: 35-44.

Weaver, S. E., and P. B. Cavers. 1979. The effects of date of emergence and emergence order on seedling survival rates in *Rumex crispus* and *R. obtusifolius*. Can. J. Bot., 57(7): 730-738.

Webber, L. R., and D. W. Hoffman. 1967. Origin, classification, and use of Ontario soils. Ontario Agricultural College publication 51. University of Guelph, Guelph, Ontario.

Weis, I. M. 1982. The effects of propagule size on germination and seedling growth in *Mirabilis hirsuta*. Can. J. Bot., 60: 186-74.

Werner, P. A. 1979. Competition and coexistence of similar species. *In* Topics in plant population biology. O. T. Solbrig, S. Jain, G. B. Johnson, and P. H. Raven (eds.). pp. 287-310. Columbia University Press, New York.

Werner, P. A. 1977. Colonization success of a "biennial" plant species; experimental field studies of species cohabitation and replacement. Ecology, 58: 840-849.

Werner, P. A. 1975a. The biology of Canadian weeds 12. *Dipsacus sylvestris* Huds. Can. J. Plant Sci., 55: 783-794.

Werner, P. A. 1975b. The effects of plant litter on germination in teasel, *Dipsacus sylvestris* Huds. Am. Midl. Nat., 94: 470-476.

Werner, P. A. 1975c. A seed trap for determining patterns of seed deposition in terrestrial plants. Can. J. Bot., 53: 810-813.

Werner, P. A. 1975d. Predictions of fate from rosette size in teasel (*Dipsacus fullonum* L.). Oecologia (Berl.), 20: 197-201.

Werner, P. A., and H. Caswell. 1977. Population growth rates and age vs. stage distribution models for teasel (*Dipsacus sylvestris* Huds.). Ecology, 58: 1103-11.

Werner, P. A., and W. J. Platt. 1976. Ecological relationships of co-occurring goldenrods (*Solidago*: Compositae). Am. Nat., 8: 1-14.

Wesson, G., and P. F. Wareing. 1969a. The role of light in the germination of naturally occurring populations of buried weed seeds. J. Exp. Bot., 20: 402-413.

Wesson, G., and P. F. Wareing. 1969b. The induction of light sensitivity in weed seeds by burial. J. Exp. Bot., 20: 414-425.

Wilbur, H. M. 1977. Propagule size, number, and dispersion pattern in *Ambystoma* and *Asclepias*. Am. Nat., 111: 43-68.

Williams, J. T., and J. L. Harper. 1965. Seed polymorphism and germination. I. The influence of nitrates and low temperatures on the germination of *Chenopodium album*. Weed Res., 5: 141-50.

Willson, M. F., and P. W. Price. 1980. Resource limitation of fruit and seed production in some *Asclepias* species. Can. J. Bot., 58: 2229-33.

Wilson, R. G., Kerr, E. D., and L. A. Nelson. 1985. Potential for using weed seed content in soil to predict future weed problems. Weed Sci., 33: 171-175.

Winn, A. A. 1985. Effects of seed size and microsite on seedling emergence of *Prunella vulgaris* in four habitats. J. Ecol., 73: 831-840.

Wulff, R. D. 1986a. Seed size variation in *Desmodium paniculatum*. I. Factors affecting seed size. J. Ecol., 74: 87-97.

Wulff, R. D. 1986b. Seed size variation in *Desmodium paniculatum*. II. Effects on seedling growth and physiological performance. J. Ecol., 74: 99-114.

Wulff, R. D. 1973. Intrapopulational variation in the germination of seeds in *Hyptis suaveolens*. Ecology, 54: 646-49.

Young, J. A., and R. A. Evans. 1973. Mucilaginous seed coats. Weed Sci., 21: 52-54.

Young, J. A., and R. A. Evans. 1972. Germination and persistence of achenes of Scotch thistle. Weed Sci., 20: 98-101.

Young, J. A., and R. A. Evans. 1969. Control and ecological studies of Scotch thistle. Weed Sci., 17: 60-63.

Young, T. P. 1984. The comparative demography of semelparous *Lobelia telekii* and iteroparous *Lobelia keniensis* on Mount Kenya. J. Ecol., 72: 637-650.

Zedler, P. H., Gauhlstorff, K., Scheidlinger, C., and C. R. Gautier. 1983. The population ecology of a dune thistle, *Cirsium rhothapikum* (Asteraceae). Am. J. Bot., 70: 1516-1527.

Zimdergren, D. 1980. The dynamics of seed banks in an area of sandy soil in southern Sweden. Bot. Notiser, 133: 633-641.

Zimmerman, J. K., and I. M. Weis. 1983. Fruit size variation and its effects on germination and seedling growth in *Xanthium strumarium*. Can. J. Bot., 61: 2309-15.

VITA

NAME:	Paul Frederick Threadgill
YEAR OF BIRTH:	1954
PLACE OF BIRTH:	Harlan, Kentucky
POST-SECONDARY EDUCATION AND DEGREES:	University of Kentucky Lexington, Kentucky 1972-1977 B.Sc., M.A.
	University of North Carolina Chapel Hill, North Carolina 1977-1979
	University of Western Ontario London, Ontario 1979-1986 Ph.D.
HONORS AND AWARDS:	Phi Beta Kappa University of Kentucky 1975
	Academic Scholarship University of Kentucky 1976
	Province of Ontario Graduate Fellowship University of Western Ontario 1980-1981, 1982-1984